TITLE PAGE

Predatory behaviour of theraphosid spiders in Northern Queensland

Thesis submitted by
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Abstract:

The predatory behaviours of three theraphosid spiders (*Selenotypus plumipes*, *Selenocosmia stirlingi*, and *Phlogiellus* sp.) from Northern Queensland, Australia, were studied using laboratory experiments and field observations. The project investigated how theraphosids detect the presence and location of prey or enemy organisms, which senses they use, and indicated how accurate these senses are. Further, the project explored whether Australian theraphosids employ a pure "sit and wait" predatory strategy, or if they will regularly leave their retreat and temporarily search for prey in a more active manner.

The importance and sensitivity of the various senses were explored in purpose-built experimental apparatus, controlling which stimuli were available to the spider. Spider behaviour was recorded using IR video. Tapes were either analysed directly or were computer-digitised for frame-by-frame analysis. For field observations the observer was seated on a vibration-dampening base and used a red light for direct observation of spider behaviour.

Importance of vision was explored by testing responses to visual stimuli in a set-up of two terrariums, vibrationally and olfactorily isolated from each other. Responses to olfactory cues were studied in a two-choice olfactometer. The ability to detect substrate related chemical cues was explored in a two-way labyrinth, while the presence of taste was tested by introducing raw meat into the terrariums. An artificial spider burrow emerging into a "test-arena" was used to record and study prey capture responses, to measure precision and distance of prey detection, as well as observing methods of prey handling. This apparatus was also used to evaluate spider responses to falling leaves, sticks and a leaf "rattling" in wind, cues characteristic of abiotic noise.

An apparatus with four "propellers" at 0, 1, 3, and 5 cm depth in a "river sand" substrate was used to test whether spiders could detect depth of burrowing "prey". Locomotory activity was studied in individual holding-terrariums and in a large container.

Spiders did not respond to visual stimuli. Similarly, reactions to airborne and substrate-related chemical cues from prey were not detected. A sense of taste is present, as the meat was eaten by 6 of 10 spiders. Responses to vibratory stimuli were complex: prey

animals were detected at least 26 cm away, but seldom attacked at distances further than 10 cm. Falling leaves often initiated attacks, whereas falling sticks and a “rattling” leaf were mostly ignored.

Responses to propellers were clear-cut: at 3 and 5 cm depth the propellers were detected but not attacked. At 1 cm depth the spiders dug down and attacked the propeller, while no digging was observed when attacking the surface propeller.

Spiders in the laboratory walked considerable distances in their terrariums (max 113m in one night), until given an artificial burrow, whereupon they, like all spiders in the field, stayed close to their retreat at all times.

In conclusion, the patterns found in laboratory and field are consistent with a picture that Australian theraphosids predominantly hunt by ambushing prey near their refuge. Prey is primarily detected by air- and substrate-borne prey-generated vibrations. Different vibrational “signatures” are detected and can influence the types of spider response. Results indicate that surface and subsurface prey have different “signatures”, detected by the spiders. Prey capture, and responses to various vibratory stimuli appear dynamic and complex, and are recommended for further research.

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STATEMENT ON SOURCES

DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

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(Name)

Chapter 1: Introduction.

Spiders are a very ancient group of animals that probably first appeared in the Devonian period, almost 400 million years ago (Selden et al. 1991 in Foelix 1996). Throughout time they have adapted to vast changes in climate and fauna, to become widespread on all continents, inhabiting nearly every terrestrial habitat, but only invading the margins of the sea. Presently 38 432 species of spiders are recognised (Platnick 2004).

Due to their massive size and striking hairiness the theraphosid spiders, commonly called "Tarantulas", are among the most widely known of the spider families, among both the general public and biologists. Theraphosids belong to the spider suborder Mygalomorphae, which consists of spiders with "primitive" morphological characteristics, such as large fangs that move parallel to the body axis, and 2 pairs of "book-lungs" for respiration. The basic mygalomorph body structure is ancient and has probably been around since the middle of the Devonian period (Foelix 1996).

Like other spiders the theraphosids suffer from being relatively unpopular among the general public. They tend to invoke a primordial fear in many people, and have been widely used in horror tales and movies. This again has given them the largely undeserved reputation as being very dangerous animals, lurking in the bush waiting to sink their fangs into an unsuspecting human victim.

This unpopularity is somewhat reflected in the very limited amount of scientific work that has been done on these spiders. Some work has been done on venom toxicity, on the special "urticating hairs" on the abdomen of American species, and on their taxonomy. The theraphosids are a widely distributed spider family with 878 recognised species (Platnick 2004). They can be found in most tropical and subtropical parts of the world, and thrive in a wide variety of habitats, from deserts to rainforests.

Little is known about most aspects of the biology of the family. Some very basic information on behaviour is known from some species, often generalised to the entire family, with little or no knowledge of the specific behaviour of most of the different species.

Theraphosids are the largest of all spiders (Costa and Pérez-Miles 2002) and some specimens can exceed 10 cm in body length (*Theraphosa blondi*) (Nyffeler et. al 2001). These giants are powerful predators with stout fangs that vie with some snakes for length (Raven 2000b on *Selenocosmia*). They can be ferocious predators and opportunistic feeders which, due to their large size and well-developed venom apparatus, enables them to prey on a wide variety of prey species. Unlike most other spiders, theraphosids are believed to prey regularly on a large variety of vertebrate prey, including rodents, birds, geckos, other lizards and even snakes. As such they are an important ecological factor, and represent the top predator of numerous food chains.

Arachnids have been found to use a variety of senses to detect their prey. Vision, taste and chemical cues have been found to have variable importance among different species. Most arachnids however, are believed to use detection of vibrations both in air and through the substrate as their primary means of detecting prey (Barth 1982). From a scientific point of view, little is known about the importance of various senses in prey capture among theraphosid spiders.

Most mygalomorph spiders like funnel-web and trapdoor spiders (families Hexathelidae, Idiopidae, Ctenizidae etc.) hunt their prey using a well-known refuge-based sit-and-wait predatory behaviour, and under normal circumstances will never venture far from their burrow (apart from adult males) (Main 1982, Bradley 1996, Shillington 2002). In contrast, theraphosids are believed to often leave their retreat and actively search for prey (Brunett, 1996). The occurrence of this roving behaviour is supported by observations that both male and female theraphosids are found wandering freely (Main 1982, Shillington 2002). This is in strong contrast to funnel-web and trapdoor spiders where only mature males are found wandering about, searching for females.

An old but reliable Australian story from 1919 tells that a chicken, one of a brood, disappeared. On the ground the farmers could see dragging marks, and following these 50 feet away, they found the dead chicken and a theraphosid spider (*Selenotypus plumipes*) that was trying to drag it down its hole (Chisholm 1919 in McKeown 1963).

It is tempting to speculate that some morphological characteristics of theraphosids may be adaptations for this more active predatory behaviour.

First, their large size probably increases the variety of prey that can be taken and also reduces their vulnerability when out in the open, by simply enabling them to fend of predators that would overpower smaller spiders.

Secondly, theraphosids have developed dense tufts of hairs on their tarsi (also found in fam. Barychelidae), that enables them to get a grip on smooth surfaces. This may assist in getting a grip on hard bodied prey like beetles, or serve locomotory needs, by enabling the spiders to walk up shear rock surfaces, tree trunks, large leaves etc.

Both the morphology and the behaviour of theraphosids is markedly different from that of araneomorph and other mygalomorph spiders. Although theraphosids are widely known to the public, and recently have become increasingly popular as “pets”, scientific knowledge of all aspects of their behaviour is scarce and hence in need of further investigation.

It is necessary to establish a basic body of knowledge covering which types of behaviours occur among theraphosids in general and among the different species. Descriptive studies are needed, describing in detail the various aspects of theraphosid behaviour at family, generic and species level. When it is known what theraphosids do, one can then conduct more detailed studies on specific behaviours, in order to explain them more fully at both the proximate and ultimate level.

From these considerations I formulated the general aims of my research:

To gain knowledge of the predatory behaviour of theraphosid spiders.

1.

Explore whether Australian theraphosids hunt strictly by a "sit and wait" predatory strategy, or regularly leave their burrows temporarily, to search for prey in the nearby area in an active manner.

2.

To investigate which senses theraphosid spiders use to detect the presence and the location of prey or enemy organisms. Further, to acquire indications of how accurate these senses are.

My purpose with this study is to gather information about the behaviour of representative Australian theraphosids, concentrating on the general aims mentioned above. I also want to develop methods and techniques needed to maintain and study these creatures both in the laboratory, and in the field.

As such, my study will increase our knowledge of predatory behaviour of Australian theraphosids, and general theraphosid behaviour. The study will hopefully serve as a foundation for more detailed studies on theraphosids. I hope my findings will be of interest and use, both to scientists, and the growing number of theraphosid enthusiasts worldwide.

Chapter 2: Spider senses and the predatory behaviour of theraphosids: a literature review.

Abstract:

Sensory systems and behaviour of arachnids are discussed, concentrating on species that are wandering predators that hunt their prey without use of silken traps, and which might be expected to have senses and behaviours similar to theraphosids.

Much work has recently been done on the use of prey-generated vibrations as primary cues for prey capture by arachnids. Arachnids as diverse as scorpions and wolf spiders have been found to have very sensitive and acute sensory systems that are still far from fully understood. Recent observations on spiders using visual senses have shown spider behaviour is far more complex than previously believed.

Little is known of the biology and behaviour of theraphosid spiders, most studies having focussed on the taxonomy of the group and on aspects associated with pet husbandry. Observations on theraphosids are discussed in the context of detailed studies on other ecologically similar arachnids.

Figure 2.1: *Phlogiellus sp.(Spider no 19).*

2.1. About theraphosids:

Fossil records of spiders are rare, but they appear to be a very ancient group of animals, the first spiders appearing about 400 million years ago in the middle of the Devonian period (Selden et al. 1991 in Foelix 1996). Fossil spiders from the later Carboniferous period are all segmented, and quite similar to the still living Mesothelae (Liphistiidae), considered the most primitive of all living spiders (Foelix 1996). Extant spider species are the result of millions of years of evolution where the spiders have adapted to new prey and enemies during the rise of insects.

Presently the two dominant spider suborders are the Araneomorphae and the Mygalomorphae. The latter have retained many plesiomorphic features, such as two pairs of booklungs and fangs moving downward in a manner similar to two pocket knives held side by side and parallel to the body axis, with the blade folding back against the bases. In Australia the Mygalomorphae includes trap door spiders (families Idiopidae, Nemesiidae, Migidae, Ctenizidae, Cyrtaucheniidae, Dipluridae), funnel web spiders (family Hexathelidae), and brush-footed spiders (families Theraphosidae, Barychelidae).

Theraphosid spiders are all generally large spiders, with most species having an adult body length of more than 4 cm. They tend to live in burrows on the forest floor, although a number of species are fully arboreal and make themselves silken retreats above ground (Stradling 1994). Unlike the araneomorphs no theraphosid is known to use silk directly to capture prey (Foelix 1996), but silken sheets or “trip lines” around the burrow entrance of some species could possibly assist in prey detection (Main 1982). Theraphosid spiders all tend to have a generally hairy appearance, with the legs and pedipalps having a dense cover of hairs of various lengths and shapes, some of which serve a variety of different sensory functions. Theraphosids are commonly known by the public as ‘tarantulas’, ‘bird spiders’ or ‘bird-eating spiders’.

American theraphosid species have a dense covering of urticating hairs on the opisthosoma; these can easily be brushed off, creating severe irritation in the eyes or on the skin of the attacker (Gertsch 1979). Theraphosids from Africa, Asia and Australia lack this defence mechanism, and seem to defend themselves with threat displays and by biting.

Theraphosids take several years to reach maturity. The males tend to live only a year or so after becoming adults, using all their energy searching for females. Females on the other hand can live for several decades. The egg sac is cared for by the female and is sometimes carried under her body (Brunet 1996, Costa and Pérez-Miles 2002).

Unlike most other spiders, female theraphosids continue to moult after reaching adulthood (Foelix 1996, Costa and Pérez-Miles 2002). This has also been reported to happen in adult males but the observation has not been confirmed scientifically. Moulting occurs from about 4 times a year as juveniles (personal observation) to about once every 2 years in large adults (Costa and Pérez-Miles 2002).

2.2. Australian theraphosids:

The Theraphosidae are represented in Australia by four genera: *Selenocosmia*, *Selenotypus*, *Phlogiellus* and *Selenostholus* (Raven 2000b), with 6 described species (Main 1985). The Australian theraphosid fauna is currently being revised by Dr R. Raven at the Queensland Museum and alterations and additions are anticipated.

Distinguishing features of the family are their large size and heavily-built bodies. They are further recognised by having dense claw tufts, heavy scopula on metatarsi and tarsi, eyes in a compact group on a tubercle, and the last segment of the spinnerets being long and thin.

Theraphosids live in deep burrows, up to 1 metre deep/long and about 3 cm in diameter. The opening does not have a door, but is sometimes sealed with a curtain of silk.

In rocky habitats theraphosids often make silken tunnels in between rocks instead of trying to dig tunnels. The building of retreats seems adapted to different habitats but I believe that a burrow in the ground is the most common type (personal observations).

The local theraphosids' ability to make sound by rubbing spines on the maxilla against bristles on the chelicerae has given them vernacular names such as 'Whistling' and 'Barking spiders'. The sound is a faint whistling or hissing sound, used when the spiders are irritated or provoked and is easily audible by the human ear (Mascord 1980).

Theraphosids are very powerful spiders, with the larger species having fangs up to 1 cm long. Their venom is deadly for cats and dogs within an hour (Raven 2000a). Humans may be affected with severe pain, headache, nausea and vomiting that last for about 6 hours (Raven 2000a), but the poison is not reported to be fatal. When provoked these spiders often tend to rear up and stand their ground instead of fleeing. They can be quite aggressive, and will definitely try to bite if further provoked (Brunet 1996).

Associated with their large size theraphosids handle a variety of different prey. Besides small insects they take frogs, lizards, geckos, large insects, and free roaming spiders. Their reputation of being bird-eating spiders is well founded on reports and observations (Chisholm 1919 in McKeown 1963). There are also published records of a theraphosid eating a small rat (Pocock 1900 on *Poecilotheria regalis* in Hillyard 1994).

Theraphosids sometimes construct silken sheets around their burrow entrance, which may serve to warn them about passing prey (Clyne 1969, Mascord 1970, Main 1982). Unlike most mygalomorphs that only grab prey within reach from the burrow, theraphosids are believed to leave their burrow and to go hunting actively for prey (Main 1982, Brunet 1996). Adult female theraphosids have been found crossing roads at night (S. Fearn 2000, pers. comm.) and trapped in pit-fall traps (L. Valentine 2001, pers. comm.). In an old but reliable report concerning *Selenotypus plumipes* (Chisholm 1919 in McKeown 1963), they have been documented to have killed a chicken about 15 metres (50 feet) away from their burrow and to have dragged it all the way back. Females of an overseas fossorial species (*Aphonopelma anax*) have also been found roaming freely (Shillington 2002).

The most frequently encountered species in Queensland are *Selenocosmia stirlingi, Selenocosmia crassipes* and *Selenotypus plumipes.*

S. stirlingi:
This is a fairly widespread species, usually occupying drier grassland areas, but also found in deserts as well as costal areas. Females reach a body length of about 4.5 cm and males about 3.5 cm. First and fourth pair of legs are nearly even in length and hairiness.

This species is probably most active in spring and late summer/fall (Kotzman 1990).

S. crassipes:

This species is most commonly found in NE and N costal areas, where it often burrows near creeks. A tropical species, *S. crassipes* is a bit larger than *S. stirlingi*, with females reaching a body length of 5.5 cm and males up to 4 cm. The first pair of legs is longest and most robust, and has long bristles and hairs.

S. plumipes:

This species is only found in NE costal Queensland and seems associated with creeks.

This is Australia's largest spider with a body length of 6 cm and a leg-span exceeding 16-cm. The 4th legs are longest, with a dense covering of long hairs.

Phlogiellus seems naturally associated with rainforest north of Innisfail. There appear to be two species, one large and one small. An apparently introduced population occurs along the banks of Ross River Townsville.

2.3. Spider senses:

2.3.1. Visual sense:

2.3.1.1. General background.

Despite spiders having several eyes, vision is believed to play only a small part in the behaviour of most spider species, their general function being to differentiate between light and dark.

There are however, a few exceptions. Jumping spiders (Salticidae) have excellent vision, actually better than any insect eye. Other hunting spiders like wolf spiders (Lycosidae), lynx spiders (Oxyopidae) and crab-spiders (Thomisidae) have also got good vision. For all these four groups, vision is much used in prey capture and recognition of the opposite sex. (Foelix 1996).

In studies by Persons & Uetz (1996a), and Persons (1999), wolf spiders (*Schizocosa ocreata,* Lycosidae) were tested with various prey stimuli. Visual or visual and

vibrational cues were used, rather than vibratory cues alone, when the spiders decided how long to forage in a certain patch.

On the other hand, when the idea that another wolf spider (*Lycosa rabiada*) used mainly visual cues for hunting fireflies at night were tested, it was found that visual stimuli elicited orientation responses in only 24% of the spiders, whereas vibratory stimuli elicited orientation responses at 85% and 100% on different substrates. This suggests that nocturnal predation in this case involves vibratory rather than visual stimuli (Lizotte and Rovner 1988).

Although theraphosid spiders are believed to use their vision only to differentiate between light and dark (Dahl and Granada 1989), the importance of visual stimuli in theraphosid behaviour has not been extensively studied.

Due to their massive body size theraphosids give the impression of having fairly small eyes. However, compared to many much smaller spider species, theraphosids have actually got quite large eyes, arranged in a group on a small "tower" (tubercle) on the top of the carapace (Fig. 2.2).

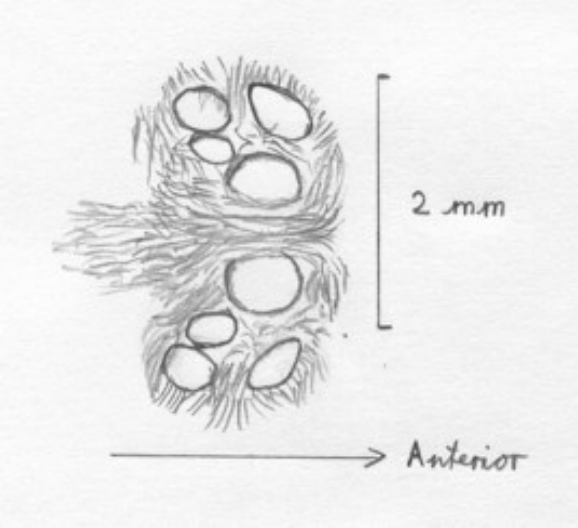


Figure 2.2: "Top-view" drawing of the eyes of a subadult theraphosid spider (*Phlogiellus sp.*). The eyes are placed on a small tower like structure, (tubercle), elevated above the prosoma.

Since theraphosids are considered to be more mobile than funnel-web and trap-door spiders, eyes could possibly be used for both detecting movement of nearby prey or predators and for navigational purposes.

Unlike jumping spiders, theraphosids do not re-orient their prosoma to enable the fixed eyes to actively observe their surroundings and particular objects (pers. obs.). I therefore find it highly unlikely that theraphosid eyes form images in the classical sense. However, known visual predators like wolf spiders also lack the distinct "prosoma

orientation behaviour" found in salticids. This probably indicates less acute vision than jumping spiders, but the lack of orientation behaviour can clearly not alone be used to assess the importance of vision in prey capture. Many Orb weavers (Araneae) have poorly-developed eyes. Still, they drop quickly out of their webs, when a predator approaches, and this is most likely a response to visual stimuli alone (Foelix 1996).

An American tarantula (*Crytopholis sp.*) was reported to respond to touch with a threat display only if approached from above, where it could see the motion. The spider held the threatening posture only as long as the object continued to move (Petrunkevitch 1952 in Laing 1975).

2.3.1.2. Structure:

The modern arachnids are the only group of arthropods in which the main organs of sight are camera-type eyes rather than compound eyes. Compared to the widely used compound eyes found in e.g. insects, camera-type eyes allow quite good resolution even in relatively small eyes, although only over a small field of view. At their best spider eyes have inter receptor angles as small as 2.4 min of arc (*Portia*). This is only six times larger than in man (0.42-min arc), and is six times better than the most acute insect eyes (14.4-min. arc in the dragonfly *Aeshna*). This level of acuity would not be achievable in a compound eye of a size that would fit on the head of a jumping spider (Land 1985).

All spider eyes are *ocelli*, or so-called simple eyes. They consist of a single cuticular lens with a cellular *vitreous body* underneath. Underneath this again are the visual cells and the pigment cells that compose the retina (Blest 1985).

The eyes are of two different types, the main eyes and the secondary eyes. Eyes are grouped into four pairs: the anterior median eyes (AME), the anterior lateral eyes (ALE), the posterior median eyes (PME), and the posterior lateral eyes (PLE).

The main eyes are always the AME. These eyes lack a reflecting layer (tapetum), and appear black. Sometimes muscles can displace the retina of the main eyes, thereby greatly increasing the field of view. Main eyes are often less sensitive in low-light conditions, and it is believed that this is due to the lack of a tapetum.

Most secondary eyes have a light-reflecting tapetum, and it is assumed that they are especially suited for seeing at night or in dim light, but this has not been extensively tested. The names main / secondary can be somewhat misleading, since secondary eyes can often be much better developed and have better resolution than the main eyes (e.g. in Lycosidae).

The secondary eyes are classified into three different types by the shape of their tapetum. (1) A primitive tapetum that fills the entire eyecup and leaves only a hole for the nerve fibres (primitive tapetum (PT)). (2) A 'canoe-shaped' tapetum consisting of two lateral walls, with a gap in the middle for nerve fibres to exit. (3) A grated tapetum that resembles the grill of an oven. The primitive type tapetum (1) is typical of "primitive" spiders e.g. the Mesothelae and Orthognatha (Mygalomorphae)(Homann 1950 in Foelix 1996). This is most likely to be the type of tapetum found in theraphosids, although I have found no specific descriptions of this.

The principal (main) eyes and the secondary eyes may have different roles in the spider's behaviour, but this is only known with certainty in the case of jumping spiders. It seems likely that the fixed secondary eyes will generally be concerned with the detection of motion relative to the spider, and the movable principal eyes with the examination of objects that do not necessarily move themselves (Land 1985).

2.3.1.3. Resolution and sensitivity:

Both resolution and sensitivity of spider eyes vary greatly between different species. Although the lenses often are of a quality that can form high-resolution images, the number of rhabdomeres (the light sensitive part of visual cells) is highly variable.

The main eyes of most spiders are small, with relatively few visual cells, and therefore not likely to detect images in the classical sense. Notable exceptions are, as previously mentioned, jumping spiders and crab spiders.

The enlarged secondary eyes of a wolf spider (*Pardosa*) contain around 4000 rhabdomeres, enabling the spider to detect images of sufficient detail to recognize its own species. At the other end of the spectrum is the small cave spider *Speocera* (Ochyrocheratidae) that has only 10 – 20 rhabdomeres, and can therefore not be expected to detect much more than movement (Foelix 1996). Unfortunately, I have not

found information regarding numbers of rhabdomeres in the main or secondary eyes of theraphosids.

Most spider eyes seem to have a high sensitivity for green, blue and UV light (reviewed by Yamashita 1985). For many species the eyes are well adapted for low-light conditions, which could be expected, as most spiders are nocturnal.

In the ctenid spider *Cupiennus salei*, an electroretinogram gave a spectral response curve with a prominent green peak at 520-540 nm and a shoulder in the ultraviolet between 340 and 380 nm, for all four pairs of eyes. The UV peak was about 65-80% of the green peak. There was also a small shoulder at about 480 nm (Blue). Most spider eyes seem to be insensitive to red light (Foelix 1996).

The threshold for corneal illuminance by white light was well below 0.01 lux. This means that *C. salei* should not only be able to use its visual senses at dusk or dawn, but also under much poorer light conditions, like moonlight (Barth et al.1993a).

Studies done on orb weaving spiders (*Argiope*) showed a very similar response curve with peaks at 360, 480, and 540 nm (Yamashita and Tateda 1983 in Yamashita, 1985). These researchers also found that the efferent neurones themselves are directly sensitive to light, their responses being significantly affected by illumination of the eyes (Yamashita, 1985). The only theraphosid studied in this respect, *Aphonopelma chalcodes*, had peak sensitivities at 500 nm (blue/green) and 370 nm (UV)(Dahl and Granda 1989).

2.3.1.4. Fields of view:

The eyes of spiders are fixed, but sometimes muscles can displace the retina relative to the lens, thereby greatly increasing the field of view (as occurs in Salticidae). The fields of view of four hunting spider families (Lycosidae, Sparassidae, Thomisidae and Salticidae) were determined by M.F. Land (1985). The fields of view of the ctenid spider *Cupiennus salei* were measured by Land and Barth (1992).

The field of view of the different eyes varies between different families as different eyes are more or less developed. Although there are a few gaps between the fields of view of the different eyes, the studied spiders all have a wide field of view covering most

angles, forward, sideways, backward, upward and slightly downward. In many families the fields of view of the ALE overlap, creating a region of binocularity that suggest one of their functions is distance judgement. The jumping spiders (Salticidae), represented by *Portia,* has the best coverage.

2.3.1.5. Polarised light:

Although many spider eyes can provide more information than once believed, most spiders have rather bad vision by human standards. Some spiders, however, can see something the vertebrate eye cannot: polarised light. Studies done on wolf spiders (*Arctosa perita*) and sheet-web spiders (*Agelena labyrinticha*) has shown that they use the patterns of polarised light in navigation. In those cases the AME were the only eyes that could analyse the plane of polarisation, the receptors involved being confined to a small part of the retina (Foelix 1996).

Lately, a new compass organ that uses polarised light has been discovered, (Dacke et al. 1999). In this case a pair of specialised secondary eyes cooperate to analyse polarised light. These eyes do not form images at all, but use a built in polarisation filter to determine exactly the direction of polarisation. Experiments indicate that the organ is most suitable for navigation at dusk and dawn, matching the fact that the spiders are primarily active after sunset.

It appears that similar organisations of the secondary eyes are found in many spider families. Preliminary studies indicate that it may be almost universally present in spiders with canoe-shaped tapeta.

Most of the above-mentioned studies have been done on jumping spiders, wolf spiders and lynx spiders that roam around to capture their prey instead of snaring them in webs (like most araneomorphs), or simply sit and wait until a prey item happens to come within reach, (like most mygalomorphs). It is therefore not surprising that the best eyes in the spider world are found among these spiders.

Theraphosids have been reported to leave their retreat to hunt actively for prey, (Main 1982, Brunet 1994), and this puts them in a situation where visual input might be more important than for most other mygalomorphs (e.g. funnel webs, trap doors).

Electrophysiological studies done on wolf spiders, jumping spiders, orb weaving spiders and net-casting spiders have revealed that spider eyes possess more complex functions than have been assumed earlier, like light sensitive nerves and detection of polarised light (see above). The visual apparatus of theraphosids, (and for most other spiders), need further studies before their physiology and behavioural importance can be known with certainty.

2.3.2. Chemical senses:

2.3.2.1. Types of chemical stimuli:

Generally two categories of chemical stimuli are distinguished, namely taste and smell, but the borderline between these categories is not necessarily very distinct. Taste involves detection of a substance directly in contact with the receptor, and often at high concentrations, whereas olfaction implies detection of much lower concentrations of volatile substances over relatively large distances (Foelix 1985). Alternative terms may be contact (taste, gustatory) and distant (smell, olfactory) chemoreception (Gullan and Cranston 1999).

In their natural environment, spiders use contact chemoreception to test the quality of food items and otherwise to determine the chemical properties of the substrate. Distant chemoreception is most likely used to find a mate during courtship and perhaps to recognise prey and enemies (Foelix 1996).

2.3.2.2. Spider chemoreceptors:

Numerous observations have shown that spiders respond to, and can differentiate between, taste and odours (olfaction) (Foelix 1985). Spiders do not have antennae, and sensors to detect chemical stimuli are instead borne mainly on the extremities. Chemoreceptor structures occur most densely on the leg-like palps and the first two pairs of legs. Chemical sensors are also distributed in much smaller numbers on all extremities, even the spinnerets.

Two types of spider chemoreceptors are recognised:

1. Contact chemoreceptors:

Chemosensory hairs are the most important spider chemoreceptors, and can be quite

numerous, e.g. over 1000 hairs have been found in an adult *Araneus* sp., primarily on the tarsi of the first legs. At first glance these hairs look similar to the common tactile hairs (Chapters 2 and 7), but arise at a steeper angle, are "S" shaped, and the tip of the hair, which is hollow, is open (Foelix 1985). The chemosensory dendrites traverse the full length of the hair, and are therefore directly exposed to the environment. These hairs probably account for the ability of spiders to determine the chemical properties of a substrate merely by probing it with their tarsi, termed "taste by touch sense", a sense also commonly found in insects. Some male spiders have about three times as many chemosensitive hairs on the palps as do females (Foelix 1996).

In addition to detecting chemical stimuli, the hair will also respond to mechanical displacement. This implies that this type of hair sensillum may have dual functions, first to register mechanical contact and then to test the chemical properties of the substrate (Foelix 1985). It is possible that these hairs also respond to some olfactory stimuli (smell) (Foelix 1996). It is tempting to speculate that the presence of mechanoreceptors on the taste hairs might enable the spider to determine whether it detects volatile (no contact) or substrate-related chemical cues (contact).

2. Distance chemoreceptors:

There is little doubt that spiders can smell, but the location of the actual olfactory organs is still not known (Foelix 1996). The tarsal organ has long been the prime candidate. This sensor can be rod-shaped, like a hair, but most often appears like a small depression or pit, and is found on the dorsal side of the each tarsus. Although this sensor was proven to react to some volatile substances (Foelix 1985), later studies by Ehn and Tichny (1994), found the primary function of this organ to be detection of changes in humidity level and temperature.

2.3.2.3. Finding mates:

It is known that spiders can use both contact and distance chemoreception to locate mates. Male lycosid spiders have been found to use contact chemoreceptors to follow pheromones on silken draglines laid down by females, by first using the pedipalps to "taste" the dragline, and then following the line by sliding the palps along either side of it (reviewed by Tietjen and Rovner 1982). It is not known whether they use taste or olfactory clues (Foelix 1996).

Recent studies show that draglines can contain a great deal of information. Female jumping spiders, *Portia* sp., discriminate between their own draglines and those from other females, and between draglines of familiar and unfamiliar conspecifics. One species, *P. labiata*, can also detect other individual's fighting ability from their dragline, a useful trait for this highly cannibalistic spider (Clark et al. 1999).

Searcy et al. (1999) used a two-choice olfactometer to study a wolf spider (*Pardosa milvina*), and found that males are able to orient themselves towards virgin females using olfactory cues only. The males were also tested using other males and penultimate instar females as olfactory cues, but this gave no response. Additional experiments involved pitfall trapping with females as bait, and this produced similar results to the olfactometer tests.

Male theraphosid spiders (e.g. *Brachypelma klaasi*) have been found to respond with short-range searching behaviours when placed near a female's burrow, probably using chemical or tactile cues to detect the presence of a female (Yanez and Locht 1999).

2.3.2.4. Locating prey:

In the context of predatory behaviour, detection of chemical stimuli has both advantages and restrictions compared to visual and mechanical stimuli:

Both airborne and substrate related chemical cues enable some predators to detect the presence of prey animals over long distances and/or when the prey is hidden from line of sight and undetectable by mechanical senses (e.g. sound). Predators following scent trails on the substrate can even locate prey animals for some period of time after they have left the area, simply by following their scent trails.

Despite the advantages of using chemical senses to locate prey, chemical stimuli cannot be used to actively scan the surroundings (like vision), and is consequently poorly suited to give precise information about the exact position of nearby prey. For prey-detecting purposes, chemical cues therefore probably serve mainly to alert the predator of the presence of prey and (together with locomotory behaviour) may allow the predator to slowly close in on the prey (Schmidt-Nielsen 1997).

In the laboratory, female wolf spiders (*Schizocosa ocreata*, Lycosidae) have been found to vary patch residence time in response to substrate-related chemical cues from insect prey. However, due to the unnaturally high number of crickets used in this experiment, it is not known whether or not this result is representative for foraging behaviour under natural conditions (Persons and Uetz 1996b). I have not found any studies exploring whether spiders can detect volatile chemical cues from prey.

Finally, it can be noted that chemical stimuli may possibly be used against theraphosids in a more offensive manner. It has been speculated that the large spider hunting wasps ("tarantula hawks", Pompilidae) secrete a chemical that somehow affect the spider so it won't react with normal predatory responses towards the attacking wasp (Petrunkevitch 1926, cited in Foelix 1996). This may account for the strange "cowardliness" or panic commonly observed in theraphosids, when attacked by these wasps.

2.3.3. Vibration detecting senses.

2.3.3.1. General background:

Many spiders live in a "world of vibrations". They use detection of different kinds of vibrations and other mechanical stimuli as their primary source of information about the surrounding environment. Spiders have developed extremely sensitive mechano-receptors, which give them accurate information about touch, air currents, substrate vibrations, and the position of individual legs and joints. All kinds of vibrations are therefore considered relevant as sources for information (Barth 1982). Most behavioural studies on spiders have been done on web-building spiders, and the vibrations generated in, and transported by, the web (Barth 1982).

However, many spider species respond to vibrations in other media: air, water, and more solid substrates. Some studies, mostly on wolf spiders, wandering spiders, and scorpions, have studied how arachnids utilise these vibrations.

Several different types of receptors have been found that detect different types of stimuli. Structurally similar receptors (e.g., the hair sensilla) may also serve quite different functions like touch and taste (Foelix 1996).

The most common mechanoreceptor is the hair sensillum, and with the addition of the short body hairs and sometimes also adhesive hairs, they make up the well-known "hairiness" of most spiders. The majority of the hairs are hair sensilla and they can number several thousands. The hair sensilla are all innervated, and can be divided into two main groups, tactile hairs and filiform hairs/trichobothria (Foelix, 1985, 1996).

Hair sensilla have a large variety of sizes and shapes, but all share the following characteristics:

(1) A hollow cuticular shaft suspended movably in a socket via an articulating membrane.

(2) Several sensory cells whose dendrites are attached to the hair shaft.

Arachnid mechanoreceptors typically have multiple innervation, whereas insect mechanoreceptors are singly innervated (Foelix, 1985). The following four types of hair sensilla have been most extensively studied in araneomorphs, and their presence on theraphosid spiders is well documented (Den Otter 1974)

2.3.3.2.Tactile hairs:

Tactile hairs are long cuticular shafts, thicker than the trichobothria, and emerge from a less developed socket. The end of the shaft is connected to three dendritic nerve endings that monitor movements, and the dendritic terminals contain a characteristic tubular body: a structure consisting of tightly-packed microtubules attached to the proximal side of the hair base.

The tubular body of insect sensilla is considered the site of sensory transduction and the tubular body of the arachnid sensilla is so similar in structure that it seems reasonable to assume the same function. The tactile hairs tend to react only to displacement of the hair from its resting position, and respond most strongly to downward motion. Apart from that they show little directional sensitivity. For a detailed description see Foelix (1985, 1996).

2.3.3.3. Spines:

Some large hairs are referred to as erectile bristles or spines. They normally lie flat along the cuticle, but can be hydraulically moved to an almost vertical position, by increasing haemolymph pressure. They only signal when being erected, and might therefore not be functioning as tactile hairs at all, but can maybe act as haemostatic pressure receptors (Foelix 1985). Other studies suggest that they are not primarily sense organs, but serve as a defensive structure protecting the spider legs from injury from struggling prey. The receptor units only provide information about the rate and degree of erection (Rovner 1980).

2.3.3.4. Scopula hairs:

These are specialised adhesive organs that give many spiders the ability to walk on vertical and even overhanging smooth surfaces, like glass. The spider may have several hundreds of these hairs on the tip of each tarsus. Each hair looks a bit like a miniature brush, with about 1000 cuticular extensions that act as points of adhesion with the substrate (reviewed by Foelix 1996). The true adhesive hairs are restricted to the tip of the tarsus. In theraphosids these are gathered in claw tufts that are coupled to the depression of the tarsal claws, and spread out to provide a larger area for contact with the substrate (Dunlop 1995). These hairs are probably primarily used for locomotory purposes (Perez-Miles 1994). For many spiders, including theraphosids, very similar hairs are found on the entire ventral side of the tarsus and often also the metatarsus. They are probably used in prey capture, by giving the spiders a good grip on large struggling prey (Rovner 1980, Dunlop 1995). Most adhesive hairs are probably singly innervated, to provide a sensory feedback when contact has been made (Foelix 1985).

2.3.3.5. Trichobothria:

The trichobothria are very fine hairs that respond to air movements and are located on the tibia, metatarsus and tarsus of the legs and on the tibia and tarsus of the pedipalps. They are from 100 to 1400 μm long and 5 – 15 μm wide and the distal portions are often bent towards the spider body (Barth et al 1993b). They can have different shapes, either long and thin or shorter and more “club” shaped (Reissland and Görner 1985). In spiders the common tactile hairs number several thousands, whereas trichobothria are much less numerous (e.g. about 900 in *Cupiennus salei*), and tend to be arranged in

straight lines or clusters on certain leg segments, in groups of from 2 to 30 hairs (*C. salei*). Often the length of the hairs varies, gradually decreasing within a group and towards the leg tip (Barth et al 1993, Reissland and Görner 1985) but I have not found studies on whether this applies to theraphosids.

Trichobothria are very sensitive, and detect even the slightest air currents (1 mm/s). The hair itself is often feathery, which increases drag forces and thus mechanical sensitivity. The hair is suspended in a socket with a very thin membrane (0.5 μm) and as such provides very little resistance towards movement. For a detailed description of the structure, see Reissland and Görner (1985).

The trichobothria's mechanical directionality can either be isotropic or have a preference for airflow parallel or perpendicular to the leg axis. Different directional properties may be combined in the same cluster of hairs. Physiologically trichobothria are tuned to frequencies between 50 and 100 Hz. and threshold deflection angles are generally 0.1°, but can be as small as 0.01°. Absolute mechanical sensitivity changes with hair length, and different hairs are thus mechanically tuned to different frequencies between 40 and 600 Hz. A cluster of hairs can thus give information about stimulus direction and also allow discrimination between different frequencies (Barth et al 1993b, Barth and Holler 1999).

Three functions have been suggested for the trichobothria: detection of air currents, air vibrations and substrate vibrations.

In the field, normal stimuli would be wind, low frequency air vibrations, like a fly buzzing near by, and possibly vibrations in the substrate such as those made by a walking insect. In the studies that have been done (see Prey detection below) trichobothria have been found to react to all three types of stimulus, but it seems they are not completely necessary for successful prey capture. Even though they do react to substrate vibrations the slit-sense organs are believed to be the main sensor for this purpose (Foelix 1996).

These findings leave the trichobothria as a system for detecting air-borne stimuli, and general alertness, probably functioning more commonly as a system to detect predators and induce fleeing. They may however be used to differentiate between different frequencies of the incoming vibrational stimulus (Foelix 1996, Reissland and Görner

1985). Recent studies by Barth and Holler (1999) suggests the trichobothria do indeed play an important part in detection of flying prey, and are directly used in prey capture. Exactly how the direction of the stimulus is detected is still not known, but some interneurons have been found to be sensitive to the direction of successive stimulation of the legs. This suggests that the direction of the stimuli can be calculated from the order in which the sensors are stimulated (Friedel and Barth 1997).

2.3.3.6. Slit-sense and Lyriform organs:

This unique mechanical sense is found only among arthropods (Barth 1985). It is a very well developed sensory system that gives the bearer a detailed picture of the mechanical events going on in its exoskeleton. It is found in insects, arachnids and crustaceans, and although the organs are morphologically different they have the same function. In insects the organ is known as the campaniform sensilla, in crustaceans simply as force-sensitive organs and in arachnids as slit-sense organs.

The slit sense organs are very specialised sensors that measure the tension in the exoskeleton that make up the hard parts of the spider's body. The exoskeleton transmits mechanical stress caused by air and substrate vibrations, gravity, changes in haemolymph pressure, or the spider's own movements (Barth, 1985).

For the slit-sense organs (and the analogous campaniform sensilla in insects) displacement is most important on the sensory level, but strain is also detected on the level of the larger skeletal region the organs are built into. Slit sensilla vary widely in respect to their arrangement in the exoskeleton and have been found to be involved in many different aspects of behaviour. Slit-sense organs are believed to be the main sensory system for detecting (among other things) substrate-related vibrations (Barth 1985).

Slit sensilla are distributed over the entire body, but are most numerous on the legs. They can appear singly, in loose groups, or in tight groups where the slits run strictly parallel to each other. In the last case they are called a *lyriform organ*. Lyriform organs are found mainly on the extremities, particularly near the joints. They are quite numerous. On a hunting spider, *Cupiennus salei*, about 3300 slit sensillae were counted, of which 86% were on the legs. Half of the slits formed 144 lyriform organs and the rest appeared singly or in small groups (Barth 1985, Foelix, 1996). Lyriform organs are

normally found close to joints and single slits normally at some distance from articulations. Both are often on the ventral side of the appendage and arranged roughly parallel to its long axis. Each slit is only 1-2 μm wide and from 8 to 200 μm long. The slit is bordered by a cuticular lip, and spanned by a thin membrane. Beneath the membrane is a bell shaped structure at the border of the exo- and mesocuticle. Each slit has two dendrites, only one of them traverses the bell shaped structure and attaches to the membrane. The tip contains the tubular body characteristic of arthropod mechanoreceptors. The slit-sense organs only signal when they are compressed, not when they are dilated. The system is highly sensitive and detects minute movements caused by vibrations. A movement of the tip of the leg by only 0.1-0.25μm (at 2-5 kHz) elicits a response (Barth 1985, Foelix 1996). In a more recent study the slit sensilla were found to be sensitive to movements of less than 0.1 nm (Stürzl et al. 2000). The lyriform organ can give a rough frequency analysis of the incoming vibratory stimuli since different frequency components elicit responses from different individual slits (Baurecht and Barth 1992).

The slit sensilla have a very important role in detecting vibrations from prey. With their extreme sensitivity they detect vibrations in many different media, for example sand, water, plants, dirt, and of course the web. In addition they can also detect airborne sound and function as a hearing organ in the classical sense (Barth 1982).

Slit sensilla have also been found to be very important for regulating locomotory movements. The slit sensilla responds to internal muscle contractions and are linked directly to the muscles, creating excitatory or inhibitory signals dependent on strain in the legs. This is more than a simple reflex action, as became clear when a crab was fitted with a shoe that created a continuous strain on the leg (Zill and Seyfarth 1996). The crab's walking movements were seriously affected, its depressor muscle prevented from working and the depressor muscles on adjacent legs were excited. Locomotion in arthropods is therefore not only controlled by the central nervous system, but also regulated by signals from the slit sensillae in the legs. These strain gauges send excitatory and inhibitory signals to leg muscles both in the leg where the sensor is, and to adjacent legs, thereby coordinating overall leg movement. This system may explain how these animals can be so fast and surefooted no matter if they have six, eight or ten legs (Zill and Seyfarth 1996).

2.3.3.7. Proprioreceptors:

Although the lyriform organ provide information about body movements, spiders have other sensory organs specialised for this purpose, such as tactile hairs, strategically located near an articulation, which bend when the leg is flexed. Many short tactile hairs gathered in a group, so-called 'hair plates', have been discovered located on the coxa, these are pressed down by the overlapping interjoint membrane during locomotion (Seyfarth 1985).

Another important group of sensory structures are the internal joint receptors. These are groups of sensory cells found inside palps and legs. In addition to registering the position of a joint, these sensors also detect the beginning, direction and velocity of changes in position of a joint(Rathmayer 1967 and Rathmayer and Koopmann 1970 in Foelix 1996). This information is utilised by the spider to perform so-called "kinaesthetic orientation", that is they remember their steps and are able to calculate their own present position relevant to where they were earlier and also relative to objects around them, such as their retreat site (see Navigation).

2.3.4. Thermal sensing:

As ectothermal organisms, spiders are dependent on regulating their position in the environment to maintain their body temperature. There is therefore little doubt that spiders can sense changing temperatures. Until recently no specific thermo-receptors were identified but the distal parts of the legs and spinnerets seemed to be most sensitive to thermal stimuli (Foelix1996).

Electrophysiological recordings from the tarsal organ of *Cupiennus salei*, (Ehn and Tichy, 1994), gave proof for temperature-sensitive cells in spiders. In these spiders the tarsal organ was found to be able to detect temperature differences as small as 0.4 ºC. In a later study (Ehn and Tichy, 1996) it was found that the spider *Cupiennus salei* had a threshold for detecting temperature changes varying from 0.6 – 0.08 °C, dependent on whether input from 1 or all 70 thermoreceptors from the 10 tarsal organs are combined.

It is also hypothesised that changes in temperature may deform the shaft of certain hair sensilla and transmit this mechanical force onto nerve endings (Foelix, 1996).

Spiders are also able to determine their internal body temperature, and tarantulas will move around and show avoidance behaviour if their body temperature rises above 32°C. (Foelix, 1996).

I have not found any studies that have tested the possibility of spiders detecting the body heat from prey or enemy organisms. For most spiders any endothermic animals will be too large to be suitable prey, hence if they detect the body heat of e.g. small mammals, it would only serve to warn them about potential predators. For large theraphosid spiders, where some species can exceed 10 cm in body length, it is a different story. Both small mammals and birds have been documented as prey and this opens up the possibility for both an offensive and defensive use of temperature detection. For the moment this is speculation, as not nearly enough is known about the temperature-detecting abilities of any spider.

2.4. Predatory behaviour/behavioural studies:

2.4.1. Prey detection and recognition:

2.4.1.1. General background:

I have concentrated on studies that deal with animals that use vibrational cues to detect and capture prey. These studies in the main consider fishing, wolf, and wandering-spiders, and scorpions. These animals all use vibrations as means of detecting what they are dealing with, and where it is. Vibratory stimuli vary in temporal patterns and frequency contents between various abiotic and biotic sources. One can say that different vibrational sources have a certain "vibrational signature" that can often be recognized by the predator, and influences behaviour. Several studies have explored the vibratory environment of scorpions and spiders that utilize vibrations propagating through diverse media like sand (Brownell 1977), plants (Barth et al.1988) water (Bleckman & Lotz 1987) and air (Barth and Höller 1999). As these animals have many nearly identical sense organs it seems safe to assume that they detect vibrations in similar ways.

Brownell (1984) studied waves and wave propagation in solids and identified four types of elastic waves. Two of these, the compressional- and shear- waves propagate spherically from the source throughout the body of the medium. Compressional waves (sound) cause particles to oscillate back and forth along the direction of propagation. Shear waves, on the other hand, involve particle motion perpendicular to the direction of propagation.

The other types of elastic waves propagate along the surface of the medium. Of these only Rayleigh waves are important. In Rayleigh waves the particles move in a retrograde ellipse in a plane parallel to the direction of travel and perpendicular to the surface of the medium. Compressional waves are found to travel faster than surface waves (Brownell 1984). These physical properties are exploited by many arachnids.

A neural model for stimulus angle determination has recently been developed, where a simple neural set-up gives an accurate estimate of stimulus direction. In both scorpions and spiders the eight legs form a roughly circular field, and the slit sensilla on each leg excites one command neuron. These eight command neurons are connected to inhibitory neurons from the three legs most directly opposite to it, forming an inhibitory triad. This creates a time window where spikes can come in, and the command neurons then "vote" what the animal should do (Stürzl et al. 2000).

2.4.1.2. Vibrations in sand:

The sand scorpion, *Paruroctonus mesaensis*, attracted the attention of researchers (e.g. Brownell 1977) by its ability to detect surface and subsurface prey in sand. Scorpions lack sophisticated visual, auditory and olfactory senses that guide many other predators. Simple experiments showed that they seemed to detect vibrations made by prey moving in the sand.

Whereas animals detect the source of vibrations in air or water by detecting the time difference of stimulation of spatially separated sensors, it was believed that in solids these time differences were too subtle to be detected. The scorpions, however, can detect vibrations from prey as far as 50 cm away, with accurate determination of both direction and distance up to 15 cm. At longer distances only the direction is determined (Brownell & Farley 1979).

It was found that the scorpion uses different types of receptors to detect different types of waves. The tarsal hairs on the underside of the scorpion's foot detects compressional waves whereas the slit sense organs located just above the joint of the tarsus and basitarsus detect surface (Rayleigh-) waves (Brownell 1977).

To detect direction and distance the scorpion might use the time delay between stimulation of the sensors nearest and farthest from the source, alternatively they may detect differences in stimulation intensity at various sensors. Since waves attenuate rapidly in sand, the sensors closest to the source should be stimulated most intensively.

For detection of direction, arrival time proved to be the major cue, and delays down to 0.2 milliseconds elicited accurate turning responses.

To detect distance the scorpion might use the attenuation of the signals, but more likely it uses the time difference between the fast moving compressional waves and the slower Rayleigh waves.

The scorpion seems to use only Rayleigh waves to sense direction. Compressional waves attenuate faster than Rayleigh waves and therefore travel shorter distances. This may explain why the scorpion can detect only direction at distances from 15 to 50 cm away (Brownell 1984).

2.4.1.3. Vibrations through plants:

The much-studied tropical wandering spider *Cupiennus salei* (Ctenidae) (Land and Barth 1992, Barth et al.1988) hunts on plants, banana plants being one of its favourites. In its vibratory environment characteristic differences in the spectral composition of vibrations from various abiotic and biotic sources were found.

Wind-generated vibrations have a very low frequency and a narrow frequency spectrum with peaks close to or below 10 Hz. Raindrops show maximal acceleration at about 100 Hz. The frequency band extends from a few Hz up to about 50 Hz for wind and to 250 Hz for raindrops.

Prey-generated vibrations are more broad banded and typically have higher frequencies. A running cockroach creates frequency spectra with peaks mostly between 400 and 900 Hz, with a frequency band extending from a few Hz up to ca. 900 Hz.

Courtship signals (vibrations produced and exchanged by courting male and female spiders) are intermediate between background noise and prey signals. Male signals typically have peaks at 75 Hz and 115 Hz, female signals between 20Hz and 50Hz.

The banana plant was found to have an attenuation value of about 0.35 dB/cm. This makes it well suited for transmitting the above signals and explains the range over which vibrations can be detected (more than 1 m observed for courtship signals) (Barth et al. 1988).

2.4.1.4. Vibrations in water:

Fishing spiders have fairly good vision (e.g. they can detect a fly 10 - 15 cm away) but visual inputs alone are seldom used for prey detection and identification (Bleckman and Lotz 1987, Bleckman and Rovner 1984).

The fishing spider *Dolomedes triton* normally hunts from the waters' edge, preying on terrestrial invertebrates that have fallen in (Bleckman and Rovner 1984). In addition they can prey on small vertebrates such as fish, frogs and tadpoles.

Air-borne vibrations, by e.g. an buzzing fly, may elicit prey capture behaviour as long as the source of the stimulus are closer than 10 cm (Bleckman & Barth 1984), but more often surface waves generated by prey struggling on the water surface triggers the prey catching behaviour. In rare occasions even hydrodynamic flow fields, generated by fish swimming nearby, triggered prey-catching attempts (Bleckman & Lotz 1987).

When in its natural environment *D. triton* may have to deal with at least 4 different vibratory stimuli: 1. From aquatic, semiaquatic, and terrestrial insect prey. 2. From small fish, frog and tadpole prey. 3. From conspecifics, and 4. From abiotic factors such as wind and falling leaves or twigs (Bleckman & Lotz 1987).

Insect-generated waves are often recognised by high frequency components (equal or greater than 50 Hz), irregular amplitude and frequency modulation, and a long duration, often more than 10 or even 60 s. (Bleckman & Barth 1984).

Vertebrate generated vibrations are more noise-like, being brief, regular in time course and with no frequencies over 40 Hz, this includes the hydrodynamic flow fields which contains predominantly frequency components below 10 Hz when created by a swimming fish.

Courtship signals from conspecifics contain components up to about 50 Hz, but rarely release prey capture behaviour. Vibratory stimuli from a falling twig or leaf tend to be brief (less or equal to1s.) and with a regular time course and constant frequency downward modulation. Wind generated waves are also more regular in their time course and rarely exceed 10 Hz. (Bleckman & Lotz 1987).

Stimuli created by aquatic and semiaquatic prey seems to be very well camouflaged in the background noise. This is supported by tests where less than 1% of fish-generated surface waves triggered prey capture attempts (Bleckman & Lotz 1987).

Generally fishing spiders *D. triton* and *D. fimbriatus* tend to localise struggling invertebrates easily, while vertebrates are harder to distinguish from the background noise. *D. triton* tends to choose fishing sites where background noise is dampened by floating vegetation (Bleckmann & Rovner 1984).

2.4.1.5. Vibrations in air:

The wandering spider *C. salei* detects and localises flying prey by using its trichobothria. Even completely blinded animals captured passing flies with a precise jump into the air. Behavioural effective range was found to be 20 cm, but the trichobothria was found to reach suprathreshold deflection level at distances up to 70 cm away from the spider. This is provided the spider is sitting on a platform, like a big leaf, which increases air speed near the surface (Barth et al 1995, Barth and Höller 1999).

In its natural environment, the background airflow has frequencies mainly below 10 Hz., and velocities below 0.1 ms^{-1}. Biological relevant stimuli, like a buzzing fly, had directionally unsteady and much higher speed flow (around 1 ms^{-1}) and a broad frequency spectrum, containing frequencies much higher than the background flow (Barth et al 1995). The trichobothria are well suited to detect and encode air particle movements created by flying prey. Due to individual tuning and a highly phasic character of their response, they provide both mechanical and physiological filtration of background flow or "noise" (Barth and Höller 1999).

In theraphosids, an African baboon spider (*Pterinochilus murinus*) has been observed to jump 10 cm straight up in the air and capture passing flies, showing a high degree of precision (personal observation). Introduction of a buzzing bumblebee into the terrarium of captive theraphosids will often elicit strong predatory reactions whereas blowing on them often leads to threat displays or fleeing behaviour (personal observation).

2.4.1.6. Vibrations from subsurface prey:

Theraphosids readily dig to capture prey (pers. obs.) It is unknown whether surface and sub-surface prey generated vibrations have different recognizable "signatures" detected by the spiders. I have not found any studies on the vibratory signals generated by sub-surface prey animals. However, it seems safe to assume that prey burrowing quite near the surface should generate both compressional and transverse waves. As the burrowing animal goes deeper, the transverse waves may become weaker until they are not detected, while compressional waves should reach the surface (depending on depth, the type of media and strength of stimulus). If this is correct, a spider may detect that compressional waves are the only ones present, thus the prey must be subsurface, probably quite deep. Another possibility is that spiders may respond to differences in strength of the different types of waves, or conclude that the prey is sub-surface simply because they are standing on top of it and cannot find it. This field awaits further studies.

For comparison, some insects are able to determine the position of sub-surface prey. Parasitic wasps (e.g. *Syngaster lepidus* and *Callibracon limbatus*) apparently use sound or vibrational cues to locate hosts inside a log, and studies suggest that they can even estimate the size of the host (Hanks et al. 2001) Another wasp, *Biosteres longicaudatus,* locates hosts inside fruits in a similar way (Gullan and Cranston 1994).

2.4.2. Communication:

Closely related to detecting vibrations created involuntarily by prey animals is the detection of communication signals sent by conspecifics. This is a large field of study, and is examined here as a means of showing that vibrations, either through air or substrate, can contain a great deal of information, both of the whereabouts of the sender, and also about who is sending and "what they want".

Small invertebrates often have relatively poor vision, and live in habitats where individuals would be obscured from each other, e.g. on separate leaves on a plant, or among foliage on the forest floor. In many cases the animals are equipped with very

sensitive vibration detectors and it has been found that vibratory communication can occur at distances of at least 1 metre (Rovner and Barth 1981).

The wandering spider (*Cupiennus*) is commonly found on banana plants in South America where it spends most of its life. It uses vibratory cues for hunting and during courtship (Rovner and Barth 1981). When the male comes across pheromone-laden silk from a female, vibratory courtship is elicited. The male starts signalling by palpal drumming and bobbing with the opisthosoma. This creates an audible airborne sound (>125 Hz), and also some hardly audible low frequency vibrations. These signals are then received by the female and she in turn signals back. This reciprocal signalling continues until the spiders find each other, the male gradually homing in on the vibrations from the female (Rovner and Barth 1981).

Pedipalpal and opisthosomal signals are quite different and serve different functions. The opisthosomal signal is a series of syllables; each syllable can be approximated to an amplitude-modulated sine wave with a carrier frequency from 60 Hz to 100 Hz. These signals possibly carry the information for species recognition, in the form of variations in temporal parameters like syllable duration, pause duration and repetition rate. Due to negligible differences in frequency content, the temporal patterns are preserved during propagation.

Palpal signals contain a wide variety of frequencies. They are not necessary to elicit a female response, and their function in courtship is not clear. However, since high frequencies attenuate faster than low frequencies, the highest frequency detectable by the female can give it some idea about the distance to the male. The sensory capabilities of the metatarsal lyriform organ are good enough for this to be possible, and this method of distance detection may also be used when hunting for prey (Baurecht and Barth 1992).

Studies of the metatarsal lyriform organ on the females, show that the signal is best interpreted by the sensor when it is within the range of the stimulus that elicit a female behavioural response (Baurecht and Barth 1993). In the wolf spider genus *Schizocosa* male courtship varies in predominantly using visual or stridulatory cues. The sensory sensitivity of conspecific females were associated with the mode of male courtship in the respective species (Hebets and Uetz 1999)

In *Cupiennius getazi* males and females tolerated large variations of amplitude, duration and repetition rate. Females didn't show any preferences between different males' signals of varying amplitudes, length, and repetition frequency. They did however show a great preference for syllables generally longer than 240 ms made up of two "sub-syllables". This is a quite species-specific pattern, differing from heterospecific signals. The signal thus serves as species recognition and does not tend to signal male quality (Schmitt et al. 1994).

Wolf spiders (*Lycosa tarentula fasciiventris*) use separate signals for courtship and agonistic interactions. Courtship signals are, like in *Cupiennus*, made by a combination of palpal drumming, and oscillations of the opisthosoma. Agonistic signals mainly involve palpal drumming. Frequencies of both signals ranges from 500 Hz to 3000 Hz, courtship signals have an energy maximum at around 1300 Hz and agonistic signals a maximum around 800 Hz. The higher frequencies in the courtship signal may be connected to distance detection as mentioned above. Courtship signals are less stereotyped than agonistic signals, and leave the possibility of female choice among male variations (Fernandez-Montraveta and Schmitt, 1994).

In another wolf spider (*Hygrolycosa rubrofasciata*) the females were found to respond more quickly to the males that signalled with a higher repetition rate and higher volume. Characteristics such as peak frequency and symmetry where not related to any other male traits. Active drumming is costly for the male (Kotiaho et al. 1988a (on energy), Mappes et al. 1996 and Kotiaho et al 1988b (on survival) both in Rivero et al. 2000) and as such gives the females an honest signal of male quality (Parri et al.1997, Rivero et al. 2000).

Web building spiders often have poor vision, and orientate themselves by interpreting vibratory signals, created by various abiotic and biotic signals and transmitted through the web (Foelix 1996, Masters and Markl 1981). This can be exploited by predators.

Probably the most advanced of all known spider communication, is done by the jumping spider *Portia fimbriata*. This spider often invades the web of other spiders, not to steal food, but to prey on the web owner itself. To manage this it uses impressive predatory strategies. It is capable of mimicking three categories of web vibrations so accurately that the web owner is fooled. *Portia* can mimic prey entangled in the web,

prey touching the periphery of the web and large-scale web disturbances. It uses prey signals to manipulate the web-owner into a striking position, and uses the artificial web disturbances to make a "smoke screen" that mask its own movement in the web (Tarsitano et al. 2000).

The use of substrate vibrations for communication is also found in insects. In two species of beetles, the male now and then signals as he moves from one area to another, probably excited by female pheromones. When a female picks up the male signal, she answers, and the males use her signals to find her. The beetles judgment of distance and direction are not so good as that found among spiders. Beetles tend to use only the intensity of the signals as clues, using klinokinesis to locate the female. That is, the male moves forward while the female stays at the same place, if the signal has become weaker the male makes a large turn and moves forward again. If the signal is stronger they make a smaller turn or stay on the same course. Vibrations are probably often used by insects to find each other on e.g. the same plant, whereas olfactory cues are used to attract mates to the right plant from longer distances (Goulson et al. 1994, Čokl et al. 1999).

Theraphosids were believed to have a very modest courtship; after direct contact the male and female had a brief interplay with their palps and front legs before copulation (Foelix 1996). More complex courtship behaviours have recently been documented. I have myself seen what clearly looks like male palpal drumming and vibrations of the body in the Mexican red kneed tarantula *Brachypelma smithi.* In *Avicularia avicularia*, a theraphosid from South America, palpal drumming and vibratory movements of the 1st pair of legs was observed in both sexes, and the male was observed to use these signals to make an female emerge from the retreat to mate (Stradling 1994).

For a North American genus, *Aphonopelma* sp. even more complex signals have been observed. The male used three different types of signalling: 1, forceful tapping with the 1st and 2nd pair of legs 2, palpal drumming and 3, a high frequency low amplitude vibration involving the whole body. Receptive females responded by leaving their burrows and walking towards the male (Shillington and Verrel 1997). Recent studies on *Brachypelma klaasi* revealed four types of signalling: 1, palpal drumming, 2, leg drumming with 1st and 2nd pair of legs 3, vibration of the whole body, and 4, "push ups" an instantaneous raising and lowering of the whole body (Yanez and Locht 1999).

Palpating or drumming has also been documented on the New Zealand mygalomorph *Porrhothele antipodiana* (Jackson and Pollard 1990).

The diversity of vibrational signals used in courtship indicates that spider senses are capable of high levels of discrimination of vibrational signals. This capability is likely to be expressed also when spiders are faced with detecting and evaluating different prey types.

2.4.3. Hunting and prey capture.

2.4.3.1. Hunting:

Most spiders and scorpions are considered to be "sit and wait" predators that ambush unsuspecting prey that come close enough for easy capture.

A few types of spider are very mobile and locate their prey from a distance before actively hunting it down, using both sneaking and deception tactics (e.g. Salticidae, *Portia*). On the other end of the spectrum are certain trap door spiders that hardly ever leave their burrow completely (Bradley 1996). Most arachnids, however, are somewhat in between these two strategies.

Many species of scorpions, most mygalomorphs, and some web-building spiders, tend to make themselves permanent homes, where they stay for most of the time relatively protected (to a lesser extent for web-builders) from wind, weather and predators.

Scorpions make simple burrows at protected sites. Ground-living spiders can make somewhat more advanced burrows, often lined with silk, and they can have side chambers, secret rooms and even hinged doors. Web builders often make silken retreats near the web periphery (Foelix 1996).

If food availability is high these animals may stay their entire life at the same place, adult males being the only ones that leave their home to search for females (Main 1982 (Mygalomorphs)). On the other hand, if food availability becomes too low, even adult females can leave their present home and search for a better location (Laing 1978 (Tunnel web spider), Shachak and Brand 1983 (Scorpion), Olive 1982 (Orb weavers)).

The sit and wait strategy is by no means as simple and straightforward as it sounds. Spatial and temporal variation in prey availability may affect foraging behaviour (Caraco and Gillespie 1986). The predator makes decisions about when and where to be hunting and how far and fast to travel. An increase in energy gain may often involve higher predation risk. The foragers' own physiological state is therefore very important

as are abiotic factors like humidity and bad weather. Individuals with a high energy-reserve are found to be most sensitive to predation risk (Skutelsky 1996).

Web-building spiders invest time and energy into making silken webs to catch prey. Then they sit and wait until a prey item get entangled in the web.

One species of orb-web spider (*Argiope trifasciata*) was found to move between several web sites as response to differences in prey availability (Olive 1982). Over an 11-day period the spiders became aggregated in areas experimentally given high prey capture rates. A noticeable drop in capture rate compared with previous nights seemed most effective in eliciting web relocation, whereas stable and sufficient capture rates tended to make them stay at the same spot for longer periods (Olive 1982).

The many arachnids that live in permanent burrows show a huge variation in locomotory activity during hunting. Some trap-door spiders do not leave their burrow unless prey are within easy reach, but can have signal threads radiating from the burrow to aid detection of passing prey (Main 1982). Other trap-door spiders are more mobile and run out of the burrow to chase passing prey (Foelix 1996). The tunnel-web spider *P. antipodiana* attaches a sheet of webbing to its tunnel entrance, and pounces on crossing prey. The sheet is very variable in size, from almost non existent under stones and logs where prey availability are considered high, to quite large and wide, (40cm), at sites where prey are scarce (Laing 1973).

Some arachnids leave their burrows at night to forage in the surrounding area by moving from ambush site to ambush site. This mode of combining mobility with the sit and wait strategy is a very efficient mode of predation and is found in free roaming predators like wolf spiders, (*Pardosa amentata*, Ford 1978), and wandering spiders, (*Cupiennus*, Foelix 1996). It is also found in species that have more permanent homes, like some scorpions (Shachak and Brand 1983), and is believed to be the case with many theraphosids (Brunet 1996).

Predatory behaviour tends to be negatively correlated with light intensity, most arachnids being nocturnal, including theraphosids although they can occasionally be active during the day (Minch 1978). Light would not directly affect the foraging behaviour of arachnids since they (most often) do not primarily rely on visual stimuli to locate their prey.

Foraging activity of the scorpion *Buthus occitanus* on dark and moonlit nights were compared by Skutelsky (1996). He found that juvenile scorpions didn't seem to alter their activity significantly, whereas adults were much less active on moonlit nights, and those adults that were active often ambushed their prey under bushes. The mass to size ratio of adult scorpions foraging in moonlight was significantly lower than in scorpions foraging on dark nights. This suggests that scorpions with relatively low energy reserves, or higher energy needs than average, chose to forage on moonlit nights even though such nights are less beneficial for foraging either due to higher predation risk from visually oriented predators or lower prey availability (Skutelsky 1996). Similar results had been found for 2 other species of scorpions (*Vejovis confusus, V. mesaensis*) in 1968, but another species (*Centruroides sculpturatus*) showed no significant response to increasing illumination (Hadley and Williams 1968). The reason for this was not determined.

Changing humidity levels may also affect predatory behaviour. Skutelsky (1996) found that an increase in humidity level tended to give higher predatory activity among scorpions (*Buthus occitanus*). It was not determined whether this is caused by increased prey activity or lower risk of dehydration.

The desert scorpion, *Scorpio maurus palmatus*, spends most of its time within one metre of the burrow, with adults having larger home ranges than juvenile scorpions (Polis et al 1985). Even in visually-oriented spiders like wolf spiders (*Pardosa amentata*), considered to be free-roaming through their habitat, locomotory activity only occurs for a minute portion (0.0032%) of each 24 h period (Ford 1978).

Very little is known about theraphosid hunting behaviour. Whether or not they actually leave their burrow and search through the environment nearby, or simply wait for passing prey at the burrow entrance is not known for certain. However, Brunet (1996) claims that Australian species regularly leave their burrows and search for prey. From time to time adult females are found wandering around but this could be due to being forced from their burrow by flooding etc. However, the earlier mentioned incident of a *Selenotypus* dragging a chicken 50 feet back to its burrow (Chisholm 1919 in McKeown 1963), is difficult to explain as anything but a successful hunting trip.

A South American theraphosid, *Avicularia avicularia,* spent the night sitting motionless within 50 cm of the retreat, reacting to vibrations from passing prey up to 25 cm away (Stradling 1994). A North American species, *Aphonopelma* sp., spent most of the time just below the lip of the burrow, but frequently left the burrow for short periods (Shillington and Verell 1997).

One might expect to find very different predation strategies among different age groups of theraphosids. A tiny 1cm-long juvenile lives a dangerous life, restricted to feeding on relatively small-sized prey, and is hunted by diverse predators. Adult spiders with a leg span of 16 cm live under completely different biotic conditions. The animal can overpower a wide variety of prey and, due to their large size, is less exposed to predators when leaving their retreat, compared with smaller spiders (Main 1982). Their venom is highly potent to large predators like cats and dogs (Raven 2000a). One might therefore expect large theraphosids to most frequently venture out of their burrows.

2.4.3.2. Prey capture:

Web weavers and free ranging hunters face different challenges in dealing with prey. Spiders that use silken traps tend to keep their distance and wrap the prey in several layers of silk until it is properly restrained. Only then do they move in close and inject venom. Hunting spiders (here meaning spiders that don't trap their prey in webs) have to grasp the prey directly, and literally grapple and fight with it to inject their venom; they then either hold on to it until the venom takes effect or track it until it dies. All the time the spider must manage to avoid any counter attacks by the prey, which can be well armed and potentially dangerous.

To help them achieve this, hunting spiders have developed both morphological and behavioural adaptations. This was studied in some detail in wolf spiders (Lycosidae) by Rovner (1980). These spiders have long legs with powerful flexor musculature to grasp and manipulate prey, and they have adhesive hairs on the legs that help them maintain a good grip on their prey. These features also serve locomotory needs.

Some of these adaptations, for example long legs, also occur in theraphosid spiders, where the legs have additional tufts of adhesive hairs on the tip of their tarsi. This is in contrast to many other mygalomorphs (like funnel webs and trap door spiders) that usually have short stumpy legs and lack claw tufts.

Rovner (1980) found that the prey of wolf spiders (in his case crickets) often struggled to free themselves, kicking at the spider using their large spined hind legs. The crickets often managed to push the spider away to the full extension of their hind feet, but as the spider had even longer legs it managed to maintain contact with the prey. During prey-capture events, the spider continuously manipulated the prey, repositioning legs that the cricket managed to kick away, and re orientated the prey relative to its own body, before using its fangs. After fang insertion the spiders tended to bend their legs away from the fighting prey, now held only by the fangs and chelicerae.

Manipulation of prey prior to striking has also been found in mygalomorphs. The New Zealand spider *Porrothele antipodiana* was found to always grasp bumblebees (*Bombus sp.*) and wasps (*Vespula germanica*) from behind the thorax and thus avoid the sting (Laing 1973). Large theraphosids on being presented a large mouse, in all cases have bitten it in the neck (pers. comm.).

When theraphosids strike they are restricted to a downward movement of their fangs. It seems to be a common assumption that they have to rear up high in order to strike, but this is not supported by observations (Laing 1975). Although the fangs are held nearly parallel to each other when in the resting position, the chelicera can swing outwards a bit, and in so doing enable the fangs to close at an angle of each other. In *Porrothele antipodiana* from New Zealand this angle has been measured to be around 60º, and each fang could swing 130º along the chelicera axis (Laing 1975). My personal observations of fang and chelicera movement in theraphosids indicate they are probably quite similar. This enables mygalomorphs to strike at most prey by elevating their body only a few degrees, so that the fangs can pass a few millimetres above the prey (Laing 1975).

For a long time it was supposed that the opposed fang action of more "modern" spiders gave them a larger span, and therefore an advantage in dealing with larger prey (Kaestner 1952 in Foelix 1996). However, experiments and observations don't support this theory (Foelix 1996). Another option is that the opposed fang action is an advantage when striking while suspended in a web in the absence of a firm substrate, but some mygalomorph spiders, e.g. *Atypus* from Britain, capture their prey by spearing it with their fangs from inside a silken "sock" lying on the ground. In this case no firm substrate between the spider and its prey is needed. Although the advantages and limitations of the two types of fang action awaits further studies, a downward

movement of large fangs seems well suited for piercing large prey against a firm surface. I have seen a juvenile *Avicularia versicolor* attack and kill a grasshopper (*Shistocerca gregaria*) nearly 3 times its size. Although it may have been a coincidence, the grasshopper was seized right on top of the thorax where the little spider was relatively safe from the powerful spiny hind legs.

2.4.4. Navigation:

2.4.4.1. General background:

When finding their way about, spiders rely on both external (allothetic) and internal (idiothetic) orientation cues. Available known external cues are optical, gravitational and mechanical cues from the substrate. Internal cues involve a behaviour known as kinaesthetic orientation, where the spiders are able to move through familiar terrain in the absence of sensory information by repetition of actions remembered from past experience of the terrain (Allaby 1999). The best-studied spider in this respect is the European *Agelena labyrinthica*, investigated by Gorner and Claas (1985).

2.4.4.2. Optical cues:

Gorner and Claas (1985) found that when *Agelena labyrinthica* leaves its retreat and runs out to catch a fly on its sheet web, it notes the position of the sun (or an artificial light source). If the light source is suddenly rotated relative to the spider when it is at its outermost point, it will head back in the "wrong" direction. Often it returns at an intermediate angle between the true angle and that given by the light source. This is due to "backup" from the kinaesthetic navigation. If the spider is gently picked up and dropped again, it is unable to use this system, and the error angle matches the moving angle of the light source more closely.

Simple experiments by rotating polarisation filters above their sheet webs have given similar results, proving that that polarised light is used to navigate (Gorner 1958, 1962 in Görner and Claas 1985). This may be a widespread capability among spiders as the recent discovery of a polarisation detection organ in eyes with canoe-shaped tapeta, which are very common, would indicate (Dacke et al. 1999).

2.4.4.3. Gravitational cues:

The direction of gravity relative to the substrate is also used for navigation. The retreat is normally the lowest part of the web. By altering the web's horizontal position *A. labyrinthica* can be made to set off in the wrong direction, towards what is now the lowest part of the web.

2.4.4.4. Substrate-related cues:

A. labyrinthica was found to also use the varying elasticity in the web for orientation. The web is usually least elastic near the retreat as the silk is thickest here. The spider simply ran along a gradient of decreasing elasticity. Experimental stretching of the web confused the spider.

2.4.4.5. Chemical cues:

How important chemical cues are for navigation is an open question. It certainly helps males find females (section 2.3.2.3), but whether it is used by spiders to return to their own retreat is unknown. In comparison, the use of both olfactory and substrate-related chemical cues for navigating is widespread in insects (Gullan and Cranston 1999).

2.4.4.6. Internal cues:

The slit sense organs and proprioreceptors are responsible for the "kinaesthetic orientation" of spiders. These organs provide the spiders with enough information about their movements to enable them to remember their own steps. For example, if a tropical wandering spider (*Cupiennus*) is gently pushed away from its newly caught prey, along a curved path, it runs back to the position where it left the prey even though the prey is removed (Seyfarth et al. 1982). It does not follow the curved path but runs back in a straight line, "cutting corners", the spider does this even when it is blinded. Thus it remembers its own steps relative to the prey and can establish the shortest way back. This mechanism probably enables spiders to find their way around in the absence of external cues (Seyfarth et al. 1982, Zill and Seyfarth 1996). On the web *A. labyrinthica* combines allothetic and idiothetic orientation cues to navigate successfully (Görner and Claas 1985).

2.4.5. Respiration rate and activity level:

Mygalomorph spiders have a primitive respiratory system, consisting of two pairs of booklungs, each of which is basically an open slit, leading to an internal atrium with several blood filled lamella, for gas exchange. In theraphosids, all blood coming from the prosoma is directed to the anterior pair of book lungs, whereas blood from the opisthosoma is directed to the posterior pair (Paul et al. 1989 in Foelix 1996). A large specimen of theraphosid (*Eurypelma sp.*) had a total lung surface area of 70 cm^2 (Reisinger et al. 1990 in Foelix 1996).

Apart from enlarging the slit opening, it is not known that the spiders can actively increase the ventilation of the lungs. Gas exchange is therefore purely by diffusion and hence set at a fixed rate, no matter what the spider's activity level is.

Spiders use hydraulic forces, created by muscles reducing the volume of the prosoma, to extend their legs. There will therefore be quite high pressure in the prosoma during periods of high activity, and consequently little oxygenated blood flowing in from the opisthosoma. It is believed that this is the reason why spiders cannot sustain high levels of activity (e.g. running) for longer time periods (Foelix 1996). Any locomotory behaviour among theraphosids can therefore be expected to involve relatively low levels of activity, (e.g. walking) if it is to continue for some time.

2.4.6. Anti predatory behaviour:

Whereas most spiders tend to retreat when confronted with a potential predator, theraphosids often rear up in an easily recognised posture. When rearing up they stand on their hind legs, holding the first and sometimes also the second pair of legs high in the air. This posture makes the spider appear larger and also gives the spider the best position to strike at an large enemy. If further provoked the spiders may open and display their large fangs, with some species (e.g. *Peterinochilus murinus*) even having small drops of poison hanging from the tip. If this posture does not deter the aggressor it is backed up with real force. The spider often reacts with powerful and lightning fast

strikes towards anything that comes close to it (personal observation). It is not known for certain whether the posture is a threat display or simply a preparation to strike. Some species, including Australian theraphosids, also make a stridulatory sound, clearly audible for humans, the function of which is unknown.

The use of similar displays may be widespread among mygalomorphs. The posture of the male Sydney funnel-web (*Atrax robustus*-Hexathelidae) is world famous and the same posture has been described for *Porrothele antipodiana* (Hexathelidae), a NZ funnel web (Laing 1975). Laing's studies also suggest that the height of rearing up is correlated with the size of the object that touched the spider.

When Laing (1975) presented *P. antipodiana* with live mice, the mice tended to attack the spider even though it reared up in display. However, if the spider managed to give a mouse a non-fatal bite the mouse retreated rapidly. When presented with another spider, several weeks later, the mouse rapidly "backed off" when the spider reared up in display.

I think the posture is primarily a display meant for large predators, since it may reduce the spiders' mobility (personal observations) and exposes vulnerable spots, such as the leg to prosoma joints and lung openings, to a small predator (Laing 1975). The posture also reduces the spiders' ability to see small animals in front of it (Laing 1975), but vision is not considered important in these spiders.

I have also experienced a large *Selenocosmia* sp. actually come out of the burrow, make stridulatory hiss and display vigorously at me in response to disturbances in the burrow entrance. Unless the posture is a display that makes most large intruders retreat, this behaviour seems maladaptive, since when the spider emerges from the burrow it makes itself more open to attack.

On being continuously harassed a *Selenotypus* sp. held in the laboratory at JCU, frequently terminated the upright posture and flipped over to its back, lying with legs outstretched and fangs gaping. This appears a very vulnerable position if attacked by small predators, but may be well suited to deliver a bite on a curious nose of a larger animal. I have not found scientific reports on this behaviour, and its function is not known.

2.5. Discussion:

Early physiological studies, revealed that arachnids had very sophisticated vibrational senses, completely different from those senses humans primarily use.

The well known jumping spider, *Portia sp*., was found to use advanced predatory strategies far beyond those conventionally expected for any invertebrate.

The anatomy of spider eyes are fairly well known, but far from understood. The image forming eyes of jumping spiders (Salticidae) have been most studied, and found to give pictures of astonishing detail. A few studies have been done on eyes of wolf and wandering spiders which, although not as good as in jumping spiders, still have good vision, and are directly used in prey capture. Other types of spider eyes have received much less attention, and often been believed to do little but differentiate between light and dark. More recent studies have revealed that they may often have quite important and complex functions, and as recently as 1999 a completely new organ that detects polarised light was discovered within spider eyes.

Much more research is needed before we understand exactly how the many very different types of eyes found in arachnids are functioning. Although most of them may not form very good images they may have important functions in detecting movement and as means of navigation.

If spider vision is poorly studied, even less is known about their chemical senses. It is known that spiders can detect both olfactory and tacto-chemical cues, but the exact location for their olfactory sensors is still unknown. The importance of olfactory cues in all aspects of behaviour needs more work, but it is known that male spiders do react to pheromones from receptive females, and can follow their silken draglines. Whether they are using olfactory or substrate-related chemical cues to follow the silken line is unknown. Jumping spiders (*Portia sp.*) can use chemical cues on the draglines of conspecifics to differentiate between individual spiders and their fighting ability. Spiders are able to detect substrate-related chemical substances with their legs.

Arachnids are very well adapted for orienting themselves without visual cues, which serves their nocturnal habits well. Chemical cues might be important, but mechanical

cues like touch, position of body relative to environment, and above all detection of all forms of vibrations, are their primary cues. They have sensors and sensory systems of remarkable complexity that enable them to navigate, build webs, hunt for prey, and avoid enemies in complete darkness.

We have gained some knowledge of the anatomy of sensors like trichobothria and slit sense organs, how they work, and their sensitivity. However, how signals from individual sensors are interpreted and integrated by the nervous system, and then in turn affect different behaviours are still far from fully understood. Arachnids are able to detect differences in frequencies and temporal patterns of incoming vibratory stimuli, and hence they can in varying degrees recognize and distinguish the different vibrational "signatures" sent out by different abiotic or biotic sources. It has been found that background noise, prey, and conspecific communication signals often have detectable differences, that are recognised by the animals.

Much more research is needed before we understand what sensory inputs the spiders receive from various sources in their natural environment, and how the behaviour of the animals are related to this.

When considering spiders that don't use webs to catch their prey, so called wanderers, most physiological and behavioural studies have been done on just a few species, notably wolf (Lycosidae), fishing (Pisauridae: *Dolomedes*) and wandering spiders (Ctenidae: *Cupiennus*).

Mygalomorphs are a particularly neglected group with reference to research on their predatory behaviour. They have been considered primitive creatures that "sit in a hole and don't do much, except eating whatever bumps into them". When consideration is taken of how long ago araneomorphs and mygalomorphs separated from the ancestral type, one might expect to find differences in sensory systems in addition to the obvious differences in behaviour.

Concerning theraphosids, the present situation is actually fairly simple. Some work has been done on taxonomy, which has given us some 800 described species, with new species still being discovered. Thanks to this effort external anatomy is fairly well known. Some very basic biology and a few aspects of their behaviour have also been described.

Apart from a few old studies in obscure literature, theraphosids have been more or less overlooked by researchers (Stradling 1994). Little is known about how these spiders hunt, overpower their prey, eat, navigate, find mates, perform courtship, deal with enemies, construct their hideouts etc.

2.6. Conclusion:

Theraphosids or "tarantulas" are among the least studied spider families, in reference to both their biology and behaviour. Some work has been done on their taxonomy. Increased research on arachnids in general reveals ever more complex senses and behaviour. Presently, researchers on behaviour of theraphosids must make their way as they go, guided only by findings on "similar species" in terms of predation strategy. These models consist mainly of free roaming spiders from the araneomorph group, and scorpions.

Chapter 3: Materials and methods.

3.1. General methods.

3.1.1. Locating spiders for laboratory experiments, and field observations.

Theraphosid spiders, here studied, are cryptic by nature. Burrow openings were often hidden in among tall grass. Spiders were located by searching through "preferred" habitats, mainly on the banks of creeks and rivers or among rocks. The spiders used in field studies were mainly found in the open eucalypt woodlands behind James Cook University. In the wet season this area is overgrown with tall grass, making it nearly impossible to search for burrows and to conduct field observations. Spiders were therefore located in the dry season, when bushfires leave the ground open. Finding enough individuals was very time consuming. On average more than 20 hours of searching was needed to find each spider, indicating that they were not very common in the area.

Spiders used for laboratory studies came from more diverse locations, mainly from the Townsville area in North Queensland, but also from Alice River (aprox. 20 km west of Townsville) and Alligator Creek (aprox. 28 km south-east of Townsville). Some of them were found by digging up burrows and searching under rocks and rotten logs. This gave some results, but proved too time consuming. An advertisement in the local newspaper made the situation much better as locals started to bring in spiders they found when digging in their gardens, cleaning the back yard etc. The provenance of all spiders used in the experiments is given in Table 3.1. Animals were identified using materials provided by Dr Robert Raven of the Queensland Museum.

3.1.2. Spider housing, handling and maintenance in the laboratory.

3.1.2.1. Housing.

All spiders where housed in individual containers. This was necessary to avoid fighting and cannibalism. Each spider was given its own terrarium, 25cm x 25cm x 45cm or larger in size. The floor was covered with a thin layer of "parrot nesting material" bought from the local pet shop. This material holds moisture quite well, but more importantly was found to reflect very little infrared light, thereby facilitating video recording under IR light.

Nr:	**Species:***	**Found at:**
1	*Selenotypus plumipes*	Townsville, JCU, Open eucalypt woodlands behind campus, with seasonal tall and dense grass. Open burrow on upper bank of seasonal creek.
2	*Phlogiellus sp.*	Townsville, JCU, Open eucalypt woodlands behind campus, with seasonal tall and dense grass. Under rock in a funnel like web in between other rocks.
3	*Selenocosmia stirlingi*	Townsville, Bohle R. Open burrows in ground among low cut grass, near road.
4	*Phlogiellus sp.*	On construction site, Magnetic Island.
5	*Phlogiellus sp.*	Dry, low-cut grass, near road 200m from Bohle River.
6	*Phlogiellus sp.*	Under big stone in a dry creek, Alligator Creek.
7	*Phlogiellus sp.*	Under tree, among rocks in a dry creek, Alligator creek.
10	*Selenocosmia stirlingi*	Unknown.
19	*Phlogiellus sp.*	Unknown.
20	*Selenotypus plumipes*	Rupertswood, Alice River.
21	*Phlogiellus sp.*	Unknown.
24	*Selenocosmia stirlingi*	Unknown.
25	*Phlogiellus sp.*	Alligator Creek.
29	*Selenotypus plumipes*	James Cook University, near creek.
35	*Selenotypus plumipes*	James Cook University, near creek.
36	*Selenotypus plumipes*	James Cook University, near creek.
37	*Selenotypus plumipes*	James Cook University, near creek.
38	*Selenocosmia stirlingi*	Kelso, near creek.
40	*Phlogiellus sp.*	Townsville, JCU,

Table 3.1: Overview of spiders used in this study for field observations or experiments:

* Taxonomy of this family is currently under revision, and there are no current published keys, some spiders classified as *Phlogiellus* sp., may therefore later prove to be a different species.

Generally Australian theraphosids are ground dwellers (Main 1985, Kotzman 1990 on *S. stirlingi*). They mostly construct their own burrows, but observations indicate they can also take over suitable refuges, like mouse nests (Fred Ford pers. comm.). To observe natural behaviour in the lab, I believe that it was necessary to allow for this, by allowing the spider to keep its retreat when moved between the different experimental set-ups. Each spider was therefore given a specially constructed retreat that could be moved from set-up to set-up, (Fig. 3.1). The retreat was made from a toilet roll, cardboard and two petri dishes.

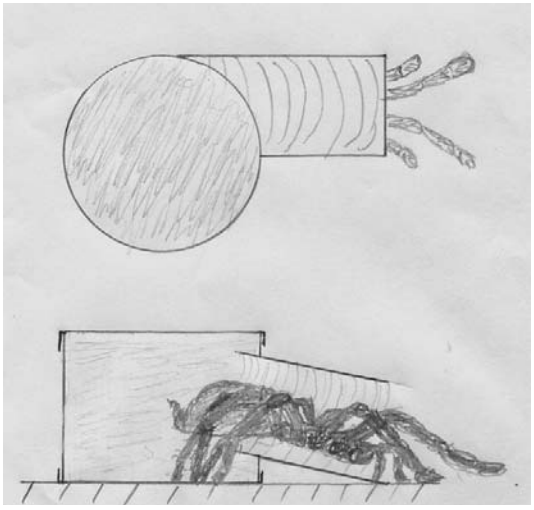


Figure 3.1: "Spider housing unit", Drawing not to scale.

By moving the entire retreat, the spider would experience being moved into a new set-up as simply a change in the surroundings, which is far less stressful than being forced into a new strange retreat.

All spiders were also given a water dish, to prevent dehydration. This was found to be necessary for captive animals when, early in the project, several spiders kept in the laboratory became severely dehydrated. In the wild they survive in arid conditions and the deep burrow probably serves a important function in ensuring a protective micro-climate (Main 1982).

3.1.2.2. Handling.

Australian theraphosids can be very aggressive. A 30cm long pair of forceps were always used when cleaning their terrarium. If it was necessary to move the spider, a lid was placed over the retreat entrance, and the whole retreat moved. Under no circumstances were the spiders handled directly. The spiders can run very fast, and escape from the terrarium in the blink of an eye. Avoiding breathing on the spider, and

using light and slow movements, normally allowed me to clean out the terrarium with no reaction from the spider. Only on two occasions did the spiders run away, both times they were sitting underneath the lid when I opened the terrarium. On both occasions the spiders were successfully recaptured with a big plastic box.

3.1.2.3. Maintenance.

The spiders were fed on a mixed diet of mealworms (*Tenebrio mollis*) and crickets (*Acheta domestica*). A few cockroaches (*Periplaneta americana*) were given, but the spiders seemed to have little success in capturing them (Chapter 7). Crickets were bought as needed, and colonies of cockroaches and mealworms were set up in the laboratory. These animals were also used as experimental stimuli.

Although vertebrates like small lizards, geckos and mice may constitute part of the spiders' diet in the wild, no such animals were used as prey animals in this study.

My pet mice, "Mousie" and "Mush Mush", were used for visual and olfactory stimuli. They were very tame, and seemed unaware of anything dangerous in this world. I therefore find it unlikely that they were subjected to any stress during the experiments.

3.1.3. General video techniques.

Australian theraphosids forage nocturnally from the burrow entrance (Kotzman 1990 on *S. stirlingi*), and will spend the majority of their time resting or sitting motionless for hours at end, waiting for prey (pers. obs.). Their vibration-detecting sensors also make them prone to detect the presence of a human observer. These factors make them poorly suited for direct observation, since:

- If the spider detects the presence of "something big" in the nearby area, it may not perform normal predatory behaviours.
- The observer may find that unmanageably long observation periods are necessary to get the required data.

By using video recordings to observe and analyse spider behaviour, the problem of being detected by the spider is eliminated, and the problems of studying theraphosid behaviour in "real time" are greatly reduced. The observer can simply fast-forward through inactive or irrelevant periods.

To ensure normal spider behaviour while recording at night, it was necessary to use infrared cameras. A standard IR surveillance camera with a built in IR light source was sufficient for all experiments. In some cases wide-angle lenses were used. Recordings where made with standard VHS video camera recorders, capable of recording at half the normal speed, thus by using 4 hour tapes an 8-hour period could be recorded.

As an additional light source I used standard LED diodes emitting IR light. Although no specific study has been done on whether theraphosids can see red or IR light, this is generally believed not to be the case. None of the spiders participating in any of the experiments showed any obvious signs of reacting to red or IR light, whereas they generally will return to their retreat when illuminated by visible light from, for example, a torch.

3.1.4. Behavioural categories used in field observation and video analysis.

By having spent considerable time observing theraphosid spiders, first as "pets" in Europe and later through preliminary studies as part of this thesis, I defined some categories used to describe some aspects of their basic behavioural repertoire to facilitate video analysis and field notes (abbreviations in parentheses). The list is not complete, and does not cover e.g. moulting and mating behaviour. I include the list as Appendix A5, as an aid to other researchers wishing to embark on field studies.

3.2. Experimental procedures and data analysis.

Although theraphosids are giants of the spider world, they are still relatively small animals. This is a great advantage when constructing various experimental set-ups, since these can be kept at a manageable scale and size for laboratory conditions.

Since the various constructions for this study were designed to be used for a limited time only, and under dry indoor conditions, it was not necessary to use weatherproof rigid materials like heavy-duty plastic or metals.

Strong cardboard, pieces of glass and plastics, held together with glue or “gaffa-tape” formed the major constituents of the various set-ups. Although it was initially a concern whether the spiders would chew their way out through the cardboard, no such attempts were observed.

Other materials included an old foam mattress, sheets of 20 mm polystyrene foam, an old computer fan, circular “hot water insulation tubes”, metal fly screen, toilet rolls, plastic petri dishes and metal string. All constructions were planned, drawn and built by the author, thereby providing adequate experimental set-ups at a very low price.

Other equipment included large plastic tubs, and a variety of different-sized glass aquaria.

3.2.1. Locomotory behaviour.

I conducted two experiments in the laboratory, and compared these results with what I found during field observations of spiders in their natural habitat.

3.2.1.1. Experiment 1: Locomotory behaviour in individual holding terraria:

Spider behaviour and activities were studied in their individual holding terraria, by video filming the spiders during their active periods at night. The terrarium was empty, apart from the spider retreat, and a water dish. A 5mm deep layer of "parrot nesting material" covered the floor.

The lid of the terrarium was replaced with a glass plate, and an infrared (IR) camera was placed such as to give a plan view of the terrarium. To avoid reflections from the light source on the glass lid, the light source was placed at an angle to the camera. Each spider was filmed for 10 hours by using 300-min standard VHS tapes on long-play recording. Recordings started at 2000 hours and ended at 0600 hours. Natural light conditions changed from dusk, to near dark, to dawn during the observation period. A total of six spiders were each filmed for four consecutive nights.

Preliminary studies quickly revealed that theraphosid spiders tend to make frequent short pauses in which their body stiffens and temporarily ceases all movement, while performing different behaviours. These short pauses are most easily recognised when the spider is walking, but also occur when the spider performs other tasks like spinning, cleaning itself or digging to construct or expand a retreat. These short breaks needed to be taken into account when determining whether the spider is "active" or "resting". It seemed that most of these temporary breaks were shorter than 10 min and the spider would then resume its previous behaviour. If the pause lasted longer, the spider would typically wait 50 to 70 minutes before moving again. I therefore decided to set a 10-min limit to the duration of the pauses I allowed for, while still considering the spider to be performing an activity like exploring the area, cleaning or spinning.

The videotapes were analysed and the following data extracted:

- The total distance (in metres) the spider walked.
- Total time (in hours and minutes) spent exploring the area. (The spider predominantly walks around, but makes frequent short pauses, none of these pauses exceeded 10min).
- Total time spent doing stationary activities, like washing or drinking, but mainly sitting completely still.
- Time spent inside the retreat.
- Time spent spinning.

The distance the spider walked was found by manually drawing the spiders' route on a scale map of the terrarium, then adding up the distances, and finally calculating the true distance walked by the spider. Although a very laborious process, this gave rather precise measurements of walking distances, and the resulting 'maps' of the spider's route, enabled careful visual inspection of the spider's movements.

Time periods were found by recording the counter reading of the VCR at the beginning of each behavioural category, and then adding up and summarising the total time for each of the selected categories.

3.2.1.2. Experiment 2: Locomotory behaviour in large terrarium.

A large terrarium: 179.5cm(L) x 34.5cm(W) x 60cm(H), was set up to mimic a forest floor (Figure 3.2). The entire floor of the tank was covered with two cm of "parrot nesting material". Several rocks, pieces of bark and some sticks were then added. One end of the terrarium was filled with large rocks, and one corner covered with rectangular pieces of thick paper, to mimic a layer of leaves. This created the following microhabitats:

1. On leaf cover.
2. Along a large stick.
3. On open ground.
4. Among rocks.

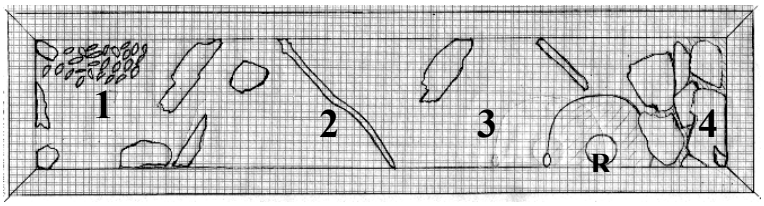


Figure 3.2: "Top-view" diagram of big terrarium, numbers correspond to microhabitats. R = Retreat.

To get plan view recordings of the entire terrarium, it was necessary to use two cameras, mounted above the tank, together with two IR light sources.

Each spider was in turn moved into the terrarium, together with its retreat. The retreat was then covered with "parrot nesting material" so that it was under ground, under a small "hill". The spider was allowed 3 days to settle in before I started recording.

Recordings started at 2000 hours and ended at 0600 hours. Natural light conditions changed from dusk, to near dark, to dawn during the observation period. Each spider was filmed for five consecutive nights, for a total of five spiders.

Video analysis was conducted as described for Study 1 (above), with the difference of simultaneously watching two screens, each covering separate halves of the terrarium, with a small overlap to facilitate tracking the spiders' movements. Time periods were also found in a similar way as above, by making sure the counters on both VCRs were synchronised.

3.2.1.3. Data analysis.

Results were only subjected to exploratory data analysis (descriptive statistics).

3.2.2. Importance of vision in prey detection.

I conducted an experiment in the laboratory to test spider responses to visual exposure to meal-beetles, cockroaches and a mouse.

In addition, relevant observations from the laboratory and in the field were discussed.

3.2.2.1. Laboratory experiment:

The basic idea of the experiment was to place spiders in a "test arena" where a visual stimulus would be visible just outside a glass wall, on one of the sides. It could then be determined if spiders visited more frequently, or spent more time in, the "stimulus half" of the "arena" than would be expected by chance.

To ensure that the spider would detect only visual stimuli, it was necessary to eliminate any vibrational cues (both through substrate and air) and olfactory cues that could enable the spider to detect the stimulus independent of vision. This was achieved by building a specially designed set-up (Figure 3.3).

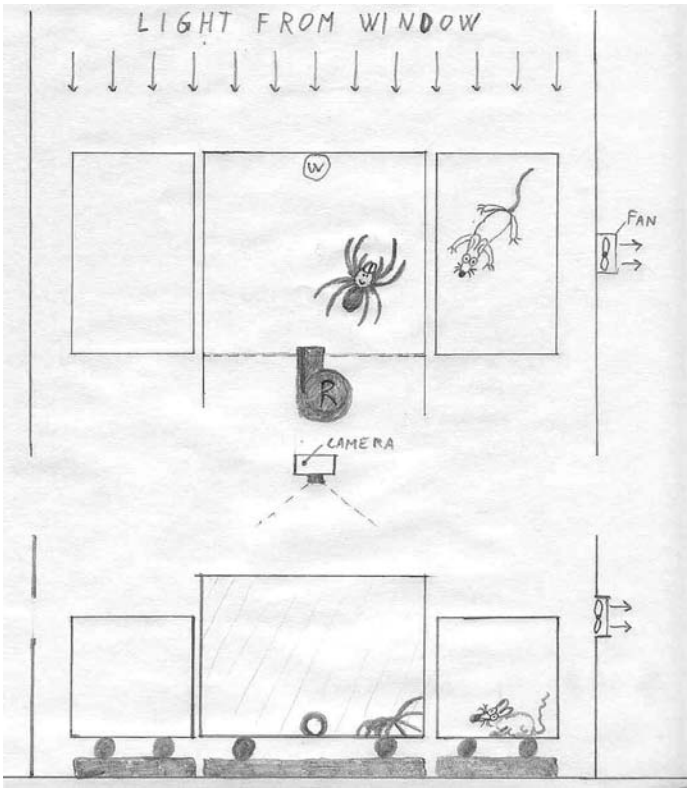


Figure 3.3: Schematic drawing of set-up to test for responses to visual stimuli. R = retreat, W = water-dish. Drawing is not to scale.

Three glass terrariums were used, two small ones, 15 cm (W) x 23 cm (L) x 15 cm (H), and one large 28.5 cm (W) x 51 cm (L) x 25.5 cm (H). The floor of all three terrariums were covered with 0.5 cm of "parrot nesting material".

One end of the large terrarium was closed off by a cardboard wall that had a 4 cm circular entrance hole cut in the middle, at floor level. This created a closed space (28.5

cm (W) x 25cm (L) x 25.5 cm (H)) for the spider to explore. Apart from a water dish placed opposite the entrance hole the "test arena" was empty.

The terrariums were arranged as shown in Figure 3.3. One of the smaller terrariums was placed on each side of the "test arena", as close to the large terrarium as possible, but without touching.

To prevent vibrations generated by the stimulus in the small terrarium from being detected by the spider in the large terrarium all terrariums where placed on top of two layers of cylindrical foam, of the type used to insulate hot water pipes. The pieces in each layer were arranged parallel to each other, and the two layers were arranged at 90^{o} to each other. This should effectively prevent any vibrations from being transferred from one terrarium to the other, in a manner in which the spider can detect stimulus direction.

The top of the terrarium containing the spider or the stimulus was covered with glass plates, resting on rubber window seals on three of four sides. The fourth side was left open, creating a narrow gap to provide air to the experimental animals. The gap of the large terrarium was towards the far short side, relative to the "test arena". The small terrarium had the gap on the long side facing away from the large terrarium.

A small computer fan, (Diameter: 60mm, 65mA, 12 V DC), was arranged so that it sucked air from around the stimulus terrarium, and blew it away from the set-up.

This was done to make sure the spider could not detect any olfactory cues from the stimulus.

The whole set-up was placed next to a window, to allow close to natural light levels.

The set-up was oriented so that the spider would face the window when it emerged, this should ensure similar light levels in all terrariums, and minimise the possibilities of reflections that would prevent the spider seeing prey in the small terrarium.

Each experimental animal was in turn moved to the large terrarium in its individual retreat. The retreat was placed so that the entrance tunnel just protruded through the entrance hole. Each spider was given 24 hours to "settle in" before recordings started.

An infrared (IR) camera with a 4mm focal length wide-angle lens, was placed directly above the "test arena", to give a plan view of the set-up. An IR light source was placed at an angle high above the set-up, between the set-up and the window, thereby avoiding reflections in the glass plates at the top of the terrariums. Each spider was filmed for 8 hours a night, by using 240-min standard VHS tapes on long play recording mode. Recordings started at 1800 hours and ended at 0200 hours. Natural light conditions changed from early dusk to near dark during the observation period. Each of five spiders was filmed for 8 nights for a total of 40 spider-nights. Four of the spiders where *Phlogiellus sp.* and in addition one *Selenotypus plumipes* was included, since this species was the dominant species in field studies but was not found in sufficient numbers to be the main species studied in the laboratory.

Five different spatial categories were used to analyse the videotapes: the spider could be inside the retreat, in the retreat entrance, in the middle of the "test arena", or on either the stimulus or control side.

The videotapes were analysed and the following data extracted:

- Whether the spider went to the stimulus or control side of the "test arena" the very first time it emerged from its retreat.
- Total number of times the spider went to the stimulus or control sides of the "test arena" as "first-choice" every time it emerged from its retreat during the night.
- Total number of visits for all five categories.
- Total time spent in all five different categories.

Activities were timed by recording the counter reading of the VCR at the point when the spider entered the relevant spatial category. Time points was then entered into a computer that accumulated the total time spent at each category.

3.2.2.2. Data analysis:

I could see no reason to expect the spiders to respond similarly to the three different stimuli. Meal beetles may be so small that they are ignored or overlooked, whereas cockroaches should be more likely to be detected, and be the right size for prey. In contrast the mouse may be viewed both as prey or a potential predator. Responses to the three different stimuli were therefore tested separately.

Tests were performed on three categories of data:

- Total number of times the spiders went to the stimulus or control sides of the "test arena" as "first-choice" every time it emerged from its retreat during the night.
- Total number of visits to the stimulus and control sides of the "test arena".
- Total time spent in stimulus and control sides of the "test arena".

The first two categories where tested on the sum of all spiders, using the Chi-Square Test of Independence, with Yates correction for continuity ($\alpha = 0.05$, $\nu = 1$).

Time-use was tested on the sum of each spider using the paired-variable t-test

($\alpha = 0.05$, $\nu = 4$). All tests were performed against an H_0 of no difference, (a 1:1 ratio of number of visits Stim / Ctrl or total time spent on Stim / Ctrl side).

Data used in analysis is available in Appendix 2, Table 1 – 3.

To determine if the spiders responded to the vibrations from the computer fan, or showed a natural bias towards turning right / left, I ran a control for each spider, with no stimulus other than the fan.

I recorded two nights for each stimulus (including the control). One night with the stimulus / fan on the right side of the test arena, and one night with the stimulus / fan on the left side.

3.2.3. Importance of chemical senses, in prey detection.

I conducted three experiments in the laboratory. Two of them were small and simple, whereas the third was more elaborate, involving a purpose-built two-choice olfactometer.

Overview of experiments:

- Experiment 1, (3.2.3.1.): Responses to dead food items, both uncovered and covered under a "mesh" so the spiders couldn't touch it directly.
- Experiment 2, (3.2.3.2.): Responses to substrate related chemical cues.
- Experiment 3, (3.2.3.3.): Responses to volatile chemical cues.

3.2.3.1. Experiment 1: Dead food items.

Several non Australian theraphosids I have kept as pets could be encouraged to grab and eat small pieces of raw meat dragged along the terrarium substrate by a thin thread.

This inspired me to explore whether theraphosid spiders would detect and eat the meat, even if it was not moving.

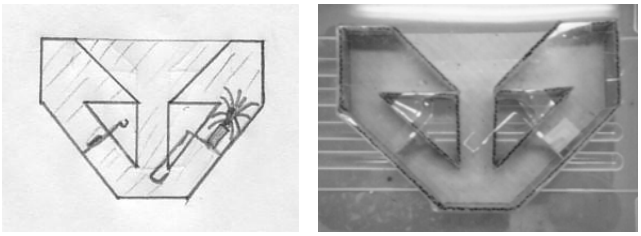
A piece of raw meat (beef) was put in a small plastic weighing dish, and placed on the substrate near the spider's retreat, inside the holding terrariums of each of 10 spiders. The meat was presented to the spiders at 1900 h, and left overnight. Great care was taken not to touch the meat or the plastic dish with bare hands, to minimize the possibilities of interfering with smell stimuli. Spider responses were observed twice, at 0200 h using a red light torch, and at 0930 h the next day. No artificial lighting was provided. Natural light entered the laboratory through the windows, and changed in intensity from dusk to dark to dawn, during the experiment.

Three days later I repeated the above-described experiment, but this time the plastic weighing dishes were "sealed" with a thin piece of paper, perforated with multiple tiny holes. This prevented the spiders from directly touching the meat, while allowing "scent-molecules" to escape. Spider responses were observed as described above.

3.2.3.2. Experiment 2: Substrate-related chemical cues.

To explore the possibilities of theraphosid spiders being able to detect and follow substrate related chemical cues from potential prey, I constructed a small two-way labyrinth (Figure 3.4), where a single entrance tunnel branched into two side tunnels, one to the left and one to the right. The side tunnels each contained a door, hinged from the roof. The doors each had a counter-weight attached, so that when they were pushed open, they would stay open. These counter weights would overlap when in the "open" position, hence the counterweight of the door that was opened first would rest underneath the counterweight of the other door if they were both opened during the night. The spiders would easily push the doors open while exploring the labyrinth (pers. obs.), hence this simple set-up could determine which side tunnel, if any, the spider explored, and in what order. The counterweights were shielded under a box (not shown in Fig 3.4), so as not to be accidentally pushed over by the spider.

Figure 3.4: Two-way labyrinth, top view. Drawing (left) and photograph (right).



A fresh scent trail from prey animals was created by closing of the left tunnel with a piece of cardboard and allowing the prey animals to roam around in the entrance and right side tunnel for 15 minutes. The prey animals and the piece of cardboard were then removed and the labyrinth placed in the spider's holding terrarium overnight. Spider responses were observed the next morning. No artificial lighting was provided. Natural light entered the laboratory through the windows, and changed in intensity from dusk to dark to dawn, during the experiment.

Ten spiders were tested with two types of chemical stimulus: large crickets (5x) and a mouse. To control for confounding effects of any chemical cues from the previous spider(s) to interfere with the results, the labyrinth was cleaned out with a wet cloth before each experiment.

3.2.3.3. Experiment 3: Olfactory stimulus.

To explore spider responses to volatile chemical stimulus, I constructed a variation of a well-known experimental set-up, termed a two-choice olfactometer. The basic idea of the experiment was to let spiders explore a Y-maze that contained a steady stream of air entering through two of the Y-maze openings, one side containing the stimulus smell, whereas the other side served as the control. It could then be determined if spiders spent more time in, or visited more frequently, the "stimulus side" of the Y-maze than would be expected from random movements. To be sure that the only cues available to influence spider movement where airborne chemical stimulus, it was necessary to eliminate any vibrational (both through substrate and air) and visual cues from the stimulus animals. This was achieved by constructing the olfactometer as shown in Figure 3.5.

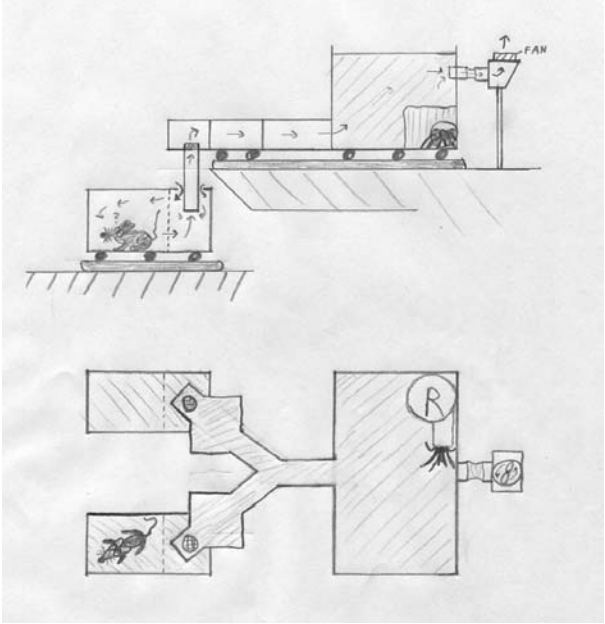


Figure 3.5: Two-choice olfactometer. Top and side view, drawing not to scale.

The set-up consisted of a large central part, holding the spider being tested, several "stimulus containers" and an self-standing "fan-unit".

The central part consisted of an "holding area", 25cm (W) x 40 cm (L) x 20 cm (H), connected to a Y-maze, 6 cm (W) x 7 cm (H) x 35 cm (L, from entrance to end of either arm). Each arm had a small chamber near the end, roughly 15 cm (W) x 15 cm (L) x 7 cm (H). At the very end of each arm a 15 cm long cylinder came up through the tunnel floor. The opening was covered by steel mesh, to prevent spiders from escaping.

The top of both the Y-maze and the holding area was covered with glass to allow observation/video recording of the spider's movements (Figure 3.6).

Stimulus containers consisted of a stimulus holding area, and a fenced off area where the cylinder from the Y-maze would enter, down through a hole in the roof. This way the stimulus animals could not touch the cylinders directly. The hole was wide enough so that the cylinder did not touch the stimulus container roof, and hence could not transfer prey-generated vibrations to the Y-maze.

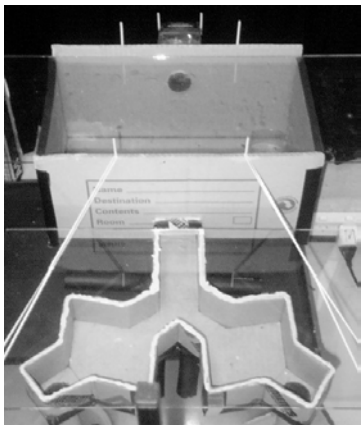


Figure 3.6: Two-choice olfactometer top\ front view.

For the control side I used a stimulus container identical to the ones containing the stimulus, so that any smell from tape, cardboard and substrate would be identical in both ends of the Y-maze, and not influence side choice.

The "fan-unit" consisted simply of a small computer fan (Diameter 60 mm, 65 mA, 12 V DC) that created slightly sub atmospheric pressure in a small chamber connected to the spider holding area via a very soft rubber hose. This way the fan would suck air from the holding area, but very little of the vibrations generated by the fan would transfer to the holding-area and Y-maze. The opening in the spider holding area was covered with a mesh to prevent spiders from escaping.

Air would flow into the "stimulus containers" through the space between the vertical cylinders and the hole in the container roof. It would then be sucked up through the cylinders, through the Y-maze, into the holding area, and finally out through the "fan unit".

The stimulus containers and the central part were placed on vibration-damping material (as described in section 3.2.2.1.), that prevented prey-generated vibrations from being detected by the spiders in a way that could influence side choice.

By the nature of the set-up, the spiders could not see the stimulus animals.

Each spider was in turn moved in its individual retreat to the holding area and given 24 hours to "settle in" before recordings started.

An infrared (IR) camera was placed above the Y-maze to give a plan view of the Y-maze and most of the holding area. An IR light source was placed at an angle high above the set-up, thereby limiting reflections in the glass. Each spider was filmed for 8 hours a night, by using 240-min standard VHS tapes on long play recording mode. Recordings started at 1900 hours and ended at 0300 hours. No artificial lighting was provided. Natural light entered the laboratory through the windows, and changed in intensity from dusk to dark during the experiment.

Five spiders was filmed for nine nights each. Four of the spiders were *Phlogiellus* sp. and in addition one *Selenotypus plumipes* was included, since this species was known to have taken vertebrate prey (Chapter 2) but was not available in sufficient numbers to be the main species studied in the laboratory.

All spiders were tested with the following stimuli: a piece of raw meat, cockroaches (*Periplaneta americana*), another spider (*Selenocosmia stirlingi*), and a mouse.

I analysed the videotapes using five different spatial categories: the spider could be inside the retreat, in the holding area, in the central part of the Y-maze, or on either the stimulus or control arm.

The videotapes were analysed and the following data extracted:

- Whether the spider went to the stimulus or control side of the Y-maze the very first time it entered the Y-maze.
- Total number of times the spider went to the stimulus or control sides of the Y-maze as "first-choice" every time it entered the Y-maze from the holding area.
- Total number of visits for all five categories.
- Total time spent in all five different categories.

Time periods were recorded by noting the counter reading of the VCR at the point when the spider entered the relevant spatial category. Time points were then entered into a computer that accumulated the total time spent at each activity.

To determine if the spiders showed a natural bias towards turning right / left, I ran a control for each spider, with no stimulus.

I recorded two nights for each stimulus, one night with the stimulus on the right side of the Y-maze, and one night with the stimulus on the left side.

3.2.3.4. Data analysis.

Results from the two small experiments were too limited to provide enough data for useful statistical analysis.

In the olfactory experiment, spiders were not expected to respond similarly to the four different stimuli. The smell of cockroaches and meat may indicate nearby potential food or prey. Meat as stimulus might increase searching behaviour, whereas cockroach smell could stimulate the spider to spend more time waiting for potential prey. The stimulus spider might be detected as a potential predator, and should then be avoided, whereas the mouse could be both a potential predator or prey, depending on the size of the spider being tested. Different stimuli were therefore tested separately.

Tests were performed on three categories of data:

- Total number of times the spiders went to the stimulus or control sides of the Y-maze as "first-choice" every time it entered the maze from the holding area.
- Total number of visits to the stimulus and control sides of the Y-maze.
- Total time spent in stimulus and control sides of the Y-maze.

The first two categories were tested on the sum of all spiders, using the Chi-Square Independence test, with Yates' correction for continuity ($\alpha = 0.05$, $\nu = 1$).

Time-use was tested on the sum of each spider using the paired-variable t-test

($\alpha = 0.05$, $\nu = 4$). All tests were performed against a H_0 of no difference, (a 1:1 ratio of number of visits Stim / Ctrl or total time spent on Stim / Ctrl side).

Data used in analysis is available in Appendix 3, table 1.

3.2.4. Function of vibration detecting senses in prey detection.

I first considered doing the experiments in natural field locations. This was abandoned due to lack of portable video and IR gear, and dependence on spider activity. For laboratory studies I constructed a special "hole in the ground set-up" to create as near "field-like" conditions as possible. Spiders were then moved one at a time to this set-up and subjected to several experiments.

3.2.4.1. "Hole in the ground set-up":

In order to make a set-up where the spider was in as near "field like" conditions as possible, while still allowing control over which stimuli were available to influence behaviour, I decided to make an artificial spider burrow in a body of hard pressed, dried dirt, inside an special closed off container (Figure 3.7).

A large plastic tub, approximately 40 cm (W) x 58 cm (L) x 45 cm (H) was clad on the inside with a 2 cm thick layer of firm polystyrene foam to dampen possible reflections of vibratory signals; the foam extended upwards around the edges of the tub, up to 15 cm from the top. To reduce the amount of dirt needed to fill the interior space, I put in a large block of styrofoam, also clad with polystyrene foam.

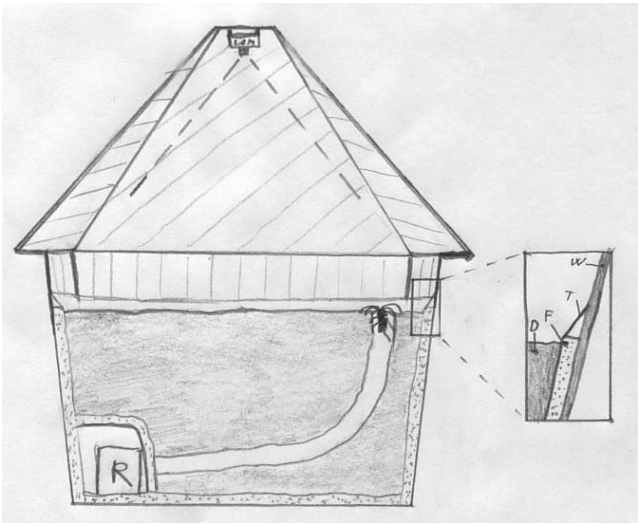


Figure 3.7: "Hole in the ground set-up" side view, drawing not to scale. D-dirt, F-foam, T-tape and W-container wall.

In the bottom right corner, I constructed a small box (also clad with foam) that would later hold the spider's retreat. A closable door gave access to the box from outside and there was a small hole in the box, leading into the interior of the container. From this hole, I extended a piece of plastic hose (4.5 cm in diameter) so that it would form an artificial tunnel through the dirt. The interior of the tub was then filled with wet soil up to 5mm below the foam, packed tight and allowed to dry. When dry, the cracks were

filled with dry soil, and the whole body of dirt moistened and allowed to dry again. This process was repeated until the block of dirt dried off without cracking.

Very carefully, I then twisted the hose loose and removed it, creating an artificial tunnel that surfaced near vertically up through the dirt, close to one of the corners. The layer of dirt was at least 20 cm thick even on top of the styrofoam block.

Figure 3.8: "Hole in the ground set-up"

To prevent unwanted air movements in the set-up I fastened a "pyramid" of heavy cardboard on top of the tub (Figure 3.8). An IR camera was fastened under the top of the pyramid, giving a plan view of the "arena".

To prevent prey animals from walking on top of the foam, following the container walls, I carefully placed an layer of brown packaging tape diagonally from the container wall, to the inner foam edge, making sure the tape would not touch the dirt. This way, prey animals were forced to walk on the substrate (except cockroaches that could climb the walls with ease). The entire structure was rested on four pieces of foam, on a concrete floor with a thin carpet.

An infrared LED light source was fastened to one side of the cardboard pyramid and together with the camera's own LED light sources provided good light for IR recordings. One side of the cardboard pyramid had a removable door for accessing the arena. The observer watched and recorded the events occurring in the "arena" by viewing the video stream from the other side of a wall.

Spiders were moved to the set-up in their retreats, and placed inside the little box so that the opening of their cardboard retreat opened out to the bottom end of the tunnel. The spiders were given four days to "settle in" before recordings started.

3.2.4.2. Experiment 1: Accuracy of spider responses to vibratory stimulus.

When the spider emerged to hunt at the burrow opening, various prey animals were released. To avoid scaring the spider this had to be done by using a special prey box (Figure 3.9). This box consisted of a bottom part, fixed to the substrate, and a top part that had an opening in the side and could be rotated from outside the set-up by pulling a fishing line. Some vertical dividers were glued to the bottom, and together with the top part, they formed several pens for prey animals waiting to be released. By very carefully pulling the fishing line, the side opening reached one pen at a time, allowing the prey to walk out at their own pace.

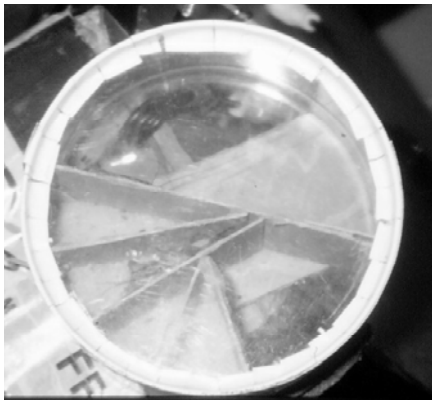


Figure 3.9: "Prey box", top view. Diameter 8 cm, height 4 cm.

Recordings started when the prey was released, and ended when the prey was captured. Relevant video sequences were loaded into a computer to enable frame-by-frame analysis of the spiders' responses. For each response still pictures from immediately before the spider started to move and just at the end of its response were extracted from the video.

From these pictures the following data was extracted using "Image Tool" software*

- **Detection distance:** The distance from stimulus to nearest part of the spider, immediately before the spider started to move.
- **Chelicera distance:** Distance from stimulus to the chelicera base of the spider, immediately before the spider started to move.
- **Rest distance:** Distance from where the stimulus was before the spider started to move, to the chelicera base of the spider at the end of its response.

* Version 3.00, The University of Texas Health Science Center, San Antonio, Texas.

- **Detection angle:** The angle from a line drawn symmetrically through the spider to the stimulus, immediately before the spider started to move. The vertex of the angle being the fovea (Figure 3.10)

- **Rest angle:** The angle from a line drawn symmetrically through the spider at the end of its response to the point where the stimulus was, immediately before the spider started to move. The vertex of the angle being the fovea.

Figure 3.10: Symmetry line and random angle.

Given that the spider spears its prey by a downward fang movement, the spider should strike so that its fangs strike down where the prey was. Hence a precise response will yield low values for rest distance and rest angle.

It should be noted that the rest angle could become very misleading when the spider orients itself so that the original prey position is inside the spider's legs. In that case rest angle was set to 0.

Based on observations of how the fangs were used during prey capture (see section 7.2.1.) distance measures were taken from the cheliceral base instead of the fang base, as this appeared to give most appropriate measurements.

No artificial lighting were provided. Experiments were done at night under near dark conditions.

Spider responses seemed naturally divided into three categories:

- Prey capture (PC).

- Prey capture response (PCR), quick response, but prey escaped.

- Prey capture movement (PCM), slow orientation towards stimulus.

It was originally planned to record captures of three meal beetles, three crickets and three cockroaches for each spider. However, meal beetles were only captured when within 1 - 2 cm from the spider, thus these captures where not suitable for measurements. Cockroaches where hardly ever captured at all. Even PCRs were rare.

The majority of measurements were therefore done on responses to crickets.

I recorded responses from a total of 5 spiders, but numbers of measurements varied greatly. Often spiders "sabotaged" the experiment by being totally inactive for several days.

3.2.4.3. Experiment 2: Responses to various "vibrational signatures".

Experiments were done in the "hole in the ground" set-up described above, and were conducted simultaneously with Experiment 1.

Spiders were given five types of abiotic stimulus:

1. Large dry leaf, roughly 7 cm in diameter.
2. Small dry leaf, roughly 4 cm in diameter.
3. Large dry stick, roughly 14 cm long and 1cm thick.
4. Small dry stick, roughly 8 cm long and 0.5 cm thick.
5. A large leaf "rattling" in wind made by a small computer fan.

The leaves and sticks (above) were dropped down on to the arena from ca 40 cm height, one at a time, when the spider emerged to hunt. Spider responses were recorded on video and, fed into a computer and analysed, as described for Experiment 1.

In order to not alarm the spider while dropping the stimuli into the arena, I glued a 5 cm piece of fishing line to the end of each stick, and to the stalk of each leaf. The fishing line was threaded through a hole in the cardboard pyramid, and fastened on the outside with a metal clip. This way, the stimulus was hanging from the roof of the arena, and could easily be dropped by carefully opening the clip.

The "rattling" leaf was put into motion by a small computer fan blowing air into the arena through the access door. To avoid fan vibrations from reaching the spider, the fan was fastened to a tripod, and was not in contact with the "hole in the ground" set-up.

Responses to rattling leaves were explored at two distances, 5 - 10 cm and 15 - 20 cm from the spider burrow.

3.2.4.4. Experiment 3: Is detection of vibrations aided by silk or other items?

This was explored by observing whether the spiders in the “hole in the ground” set-up constructed silken sheets, and determining if these sheets influenced prey detection capabilities. If silken sheets were constructed, they were removed after recordings for Experiment 1 and 2 were finished, and the spider would be given additional prey animals. These captures was compared to those with an intact web, to determine if detection distance and response accuracy had diminished.

Field observations investigated whether silken sheets were constructed in the wild.

3.2.4.5. Data analysis.

Both numbers of individual observations and number of replicates were too limited to allow for sensible use of quantitative statistically analysis. The results would at best be very unreliable.

Simple exploratory statistical analysis appeared sufficient to indicate answers to the questions in section 7.1 and reveal any clear trends.

3.2.5. 3D detection of prey stimulus position.

I would have preferred to do this experiment with live prey animals as the stimulus. However, I could see no way of ensuring that e.g. a mealworm would stay at the right depth in the substrate, and move when it had to. I therefore decided to build a specially designed set-up, where I would test the spider's responses to small moving "propellers" at various depths in a suitable substrate.

3.2.5.1. "Propeller set-up":

The set-up was made of very heavy cardboard (1 cm thick) and consisted of a closed-in basin with river sand that had four propellers mounted at various depths in the substrate.

The basin measured roughly 13 cm (H) x 37 cm (W) x 26 cm (L) less a 9 cm x 10 cm square at each rear corner (Fig. 3.11). The inside of this basin (side and bottom) was clad with ca 2 cm thick layer of foam, to dampen any reflections of vibratory signals that may confuse the spiders. The walls extended upwards from the basin another 27 cm and were extended in one direction to give enough room to place the video camera inside the set-up. The top part measured roughly 37 cm (W) x 63 cm (L). A large glass plate functioned as a lid, ensuring that air-movements in the laboratory could not interfere with the experiment.

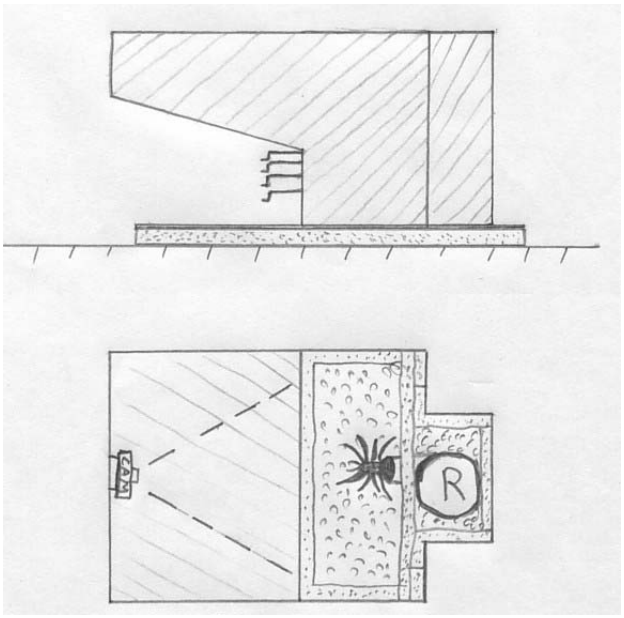


Figure 3.11: "Propeller set-up", top and side view. Drawing not to scale. R = retreat, CAM = camera.

Four "propellers" were made up of light wire, bent into a 1 cm propeller at the end of a 15 cm long shaft, with a swivel at the end. I simply drilled four small holes through the cardboard wall and foam to mount the propellers at surface level and at 1, 3, and 5 cm depths in the substrate. Some electrical tape wound around the propeller shaft

functioned as a washer and prevented the propeller from being pushed into the basin when turned. The propellers were placed about 3 cm into the basin. Great care was taken to have the propeller shafts as straight as possible to ensure that only limited vibrations would be generated by the turning propeller shaft (Fig. 3.12).

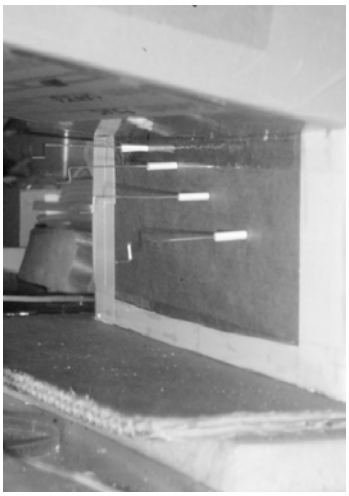


Figure 3.12: Close up view of the propeller handles.

A small IR camera with a built in LED, IR light source was placed in the end of the extended top section, facing the basin. The basin was filled with "river sand" consisting of slightly rounded large sand grains (r = ca 3 mm) up to the level of the surface propeller. A large sheet of 2 cm thick foam was placed upright to the rear of the set-up.

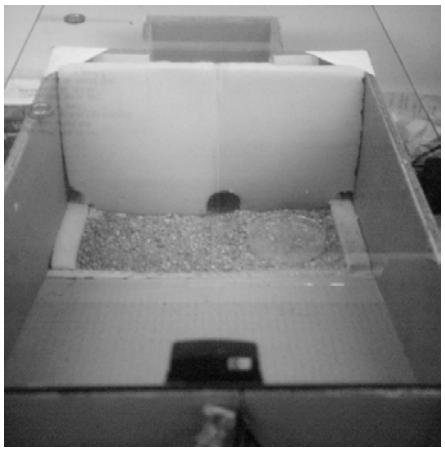


Figure 3.13: Top/front view of the "test arena" rear of camera visible in front.

The spider's retreat would in turn be placed on top of the river sand to the rear of the set-up, with only the entrance tunnel emerging into the "test arena" through a hole in the sheet of foam (Fig 3.13).

Finally, the entire construction was standing on top of a large cardboard plate resting on a layer of foam, to dampen any background vibrations.

The IR camera was connected to a TV monitor and VCR for recording the spider's responses on standard VHS videotapes. Before and during the experiment, the light in the laboratory was turned off, experiments were done at night under late dusk to near dark conditions.

Spiders were moved to the set-up one at a time, together with their retreat. In the evenings I observed the arena in the monitor, and the experiment started when the spiders, at their own pace, emerged from their retreat. The propellers were used to mimic prey under the following guidelines:

- Rotated at varying speed, in arbitrary combinations of ¼, ½ and whole turns, with short pauses of various duration (0,5 - 5 sec) in between.

- In the case of no visible reaction from the spider, the propeller was rotated for 10 minutes. If the spider responded with orientation responses, the propeller was rotated for a total of 15 minutes, or until the spider attacked the propeller.

- The propellers were turned in the following order: 5 cm - 3 cm - 1 cm - 0 cm, with a 3 minute pause between each propeller.

By turning the propellers at gradually decreasing depths, I hoped to mimic a burrowing prey making its way up to the surface.

Great care was taken not to touch the set-up while turning the propellers, as this could have influenced spider behaviour.

I tried not to "overdo" the vibratory stimulus but to keep it dampened so that it sounded (as far as I can judge) the way a burrowing mealworm sounds when I have listened to them digging in the terrariums of my pet spiders.

All spider responses were recorded on video, and later analysed by watching the responses in slow motion or frame-by-frame analysis.

3.2.5.2. Data analysis.

Spider responses to the various propellers were so clear-cut that I could see no need for quantitative statistical analysis, to answer the question outlined in section 8.1.

3.3. Field observations:

Field observation of spider behaviour were undertaken in two separate sequences, one in the dry season, (22 Oct to 30 Nov 2001), and one in the wet season, (19 Feb to 28 Feb 2002).

The spiders studied were all in Townsville. All spiders had been located in the undeveloped woodland just behind the university campus, apart from one spider that was located at the Bohle River, in a similar habitat. The spiders located were six *Selenotypus plumipes*, one *Selenocosmia stirlingi* and two *Phlogiellus* sp. The *Phlogiellus* sp. were found in Aug 2002 and therefore were studied in the second sequence only.

Spiders were observed for four nights in succession, 8 hours per night, starting at 1900 hours and ending at 0300 hours. Light conditions were generally dusk to dark, with variable amounts of moonlight. Air temperature at surface level was measured every hour, and general weather patterns (including moon phase and cloud cover) were noted.

Observations were made by using a standard Maglite 3D-cell flashlight (22 000 PBC without filter), fitted with a red filter as it is commonly believed that these spiders cannot see red and infrared light. The torch was mounted on a tripod, and provided enough light to observe a circle roughly 50 cm across, centred on the burrow entrance. Eighteen standard ni-cad rechargeable batteries allowed for 8 hours use.

All spiders are very sensitive to vibrations. To dampen any observer-generated vibrations that could affect the spider's behaviour, the observer was sitting in a camp chair, resting on a plywood plate, on top of a foam mattress (Fig 3.14). The observer was seated at 1.5 – 2 meters from the spider burrow, to allow observations of some details. Great care was taken to be as quiet as possible when changing batteries in the torch, so as not to disturb the spiders.

Figure 3.14: Vibration dampening "observation post".

Chapter 4: Locomotory behaviour.

4.1. Introduction:

The basis for these experiments were that female theraphosids of ground dwelling species normally inhabiting burrows, are sometimes encountered roaming freely (Main 1982, Shillington 2002). It is not known whether they do so voluntarily in search for prey, or have simply been forced to leave their burrow. These movements are in contrast to the well-documented male "wandering" in search of females.

Considering that theraphosids are relatively large predators, with an appetite during growth or pregnancy, prey availability in the immediate proximity of the refuge may be too low. Temporarily leaving their retreat to search through the area surrounding the burrow might increase prey availability while, during inactive periods, the spider still exploits the advantages of a permanent refuge.

Being large spiders, theraphosids may be less vulnerable when out in the open than smaller spider species (Main 1982). Also, theraphosids have long powerful legs that seem well adapted for walking (pers. obs.). Considering this together with the single report (Chisholm 1919) of prey being dragged back to a retreat, the locomotory behaviour of female and sub adult Australian theraphosids, in a context of predatory behaviour, needed further investigation.

No scientific study has as yet explored whether ground dwelling female or sub adult theraphosids temporarily leave their burrows to actively hunt for prey in the nearby area. If found, the presence of this more active predatory behaviour will clearly separate theraphosid behaviour from most other members of the infraorder Mygalomorphae.

I formulated two specific questions:

1. Do these spiders temporarily leave their burrow to actively hunt for their prey?

Hypotheses:

H_0: They only wait near the burrow entrance, and grab at passing prey.

H_1: They temporarily leave their burrow and actively seek out their prey.

Predictions: Observations of spiders, both in captivity and in the field, should find that most individuals regularly leave their burrow and wander in search for prey, returning home for their inactive periods.

2. If found to wander in search of prey, how do they hunt?

- **2.a. Are the movements random or ordered?**

Hypotheses:

H_0: They only move around by random movement.

H_1: They search through the area surrounding the burrow, in a more orderly fashion.

Predictions:

Recording and studying the movements of the spiders, should reveal whether there are recognisable patterns and various areas in a uniform habitat should ideally not be visited more than one time for each time the total area is searched.

- **2.b. Is hunting mainly done from ambush sites?**

Hypotheses:

H_0: They continuously move around during the hunt.

H_1: They move from ambush site to ambush site

Predictions:

The spiders should be found to spend most of their time ambushing for prey at various locations, with relatively short locomotory periods in between, to move from one ambush site to another.

- **2.c. Is there a microhabitat preference?**

Hypotheses:

H_0: The spider is indiscriminate of where to hunt / ambush prey.

H_1: The spider prefers certain types of microhabitats from where to hunt / ambush prey.

Predictions: Spiders should spend more time searching/ambushing for prey in some microhabitats compared to others.

4.2. Results:

4.2.1. Experiment 1: Locomotory behaviour in small individual holding terraria:

All six spiders where found to leave their retreat and explore the terrarium (Figure 4.1) wandering about on the floor, on the sides, and in rare cases even upside down on the glass plate covering the terrarium. On average they would wander around and explore the terrarium every 3.16 out of 4 nights (Table 4.1). Out of a total of 24 nights, spiders where totally inactive in 5 nights, where they stayed inside the retreat for the entire recorded period. Inactive nights are excluded from calculations. Walking distance was measured from 2.38 m up to 113 m per night. One individual spider (Nr.7) walked much longer distances than the other experimental animals (Figure 4.1). Spiders moved 20.65 m on average, but with a median of only 4.74 m (Table 4.1).

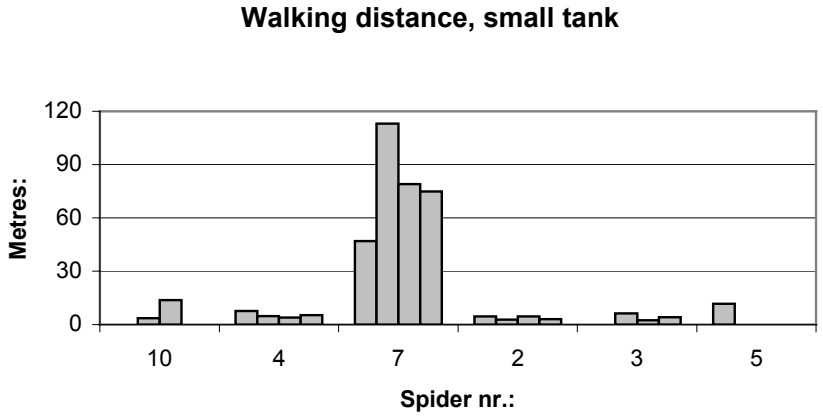
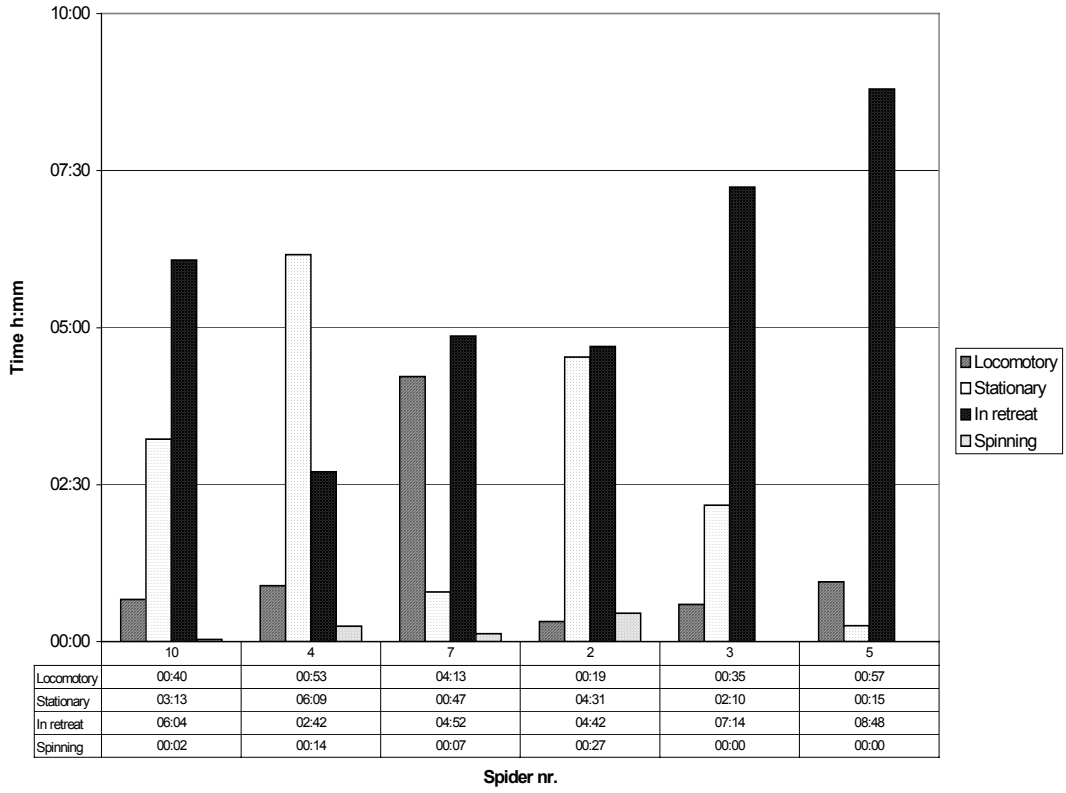


Figure 4.1: Walking distances for individual spiders, observed when studied for four nights in succession, in their individual holding terraria. Inactive nights included.

When examining temporal distribution between different behavioural categories (locomotory, stationary, in retreat, and spinning) there was no clear trend, but rather large variations both between and within individual spiders. Generally the spiders spent less time on locomotory behaviour compared to stationary behaviours and time in the retreat. All spiders spent relatively little time spinning (Table 4.1). As with walking distance, time spent on locomotory behaviour by spider nr.7 was clearly different from the rest of the group (Fig. 4.2)



	10	4	7	2	3	5
Locomotory	00:40	00:53	04:13	00:19	00:35	00:57
Stationary	03:13	06:09	00:47	04:31	02:10	00:15
In retreat	06:04	02:42	04:52	04:42	07:14	08:48
Spinning	00:02	00:14	00:07	00:27	00:00	00:00

Figure 4.2: Temporal distribution between behavioural categories, mean values for each individual spider as observed in individual holding terraria.

Table 4.1: Measures of tendencies from individual terrariums, calculated from total number of active nights (n=19), (* = calculated from all nights, n=24).

	Min.	Max	Mean	Median
Walking distance (m)	2.38	113	20.65	4.74
Nr. of 4 nights spent exploring*	1	4	3.16	3.5
Locomotory behaviour (h:min)	0:00	5:31	1:23	0:42
Stationary behaviour (h:min)	0:00	9:25	3:16	2:24
Inside retreat (h:min)	0:00	9:55	5:08	4:46
Spinning (h:min)	0:00	0:52	0:10	0:05

Careful studies of the recordings and visual comparison of the spiders' walking pattern did not reveal any clear search pattern. All spiders clearly gave the impression of being limited in their movements by the terrarium. A lot of time was typically spent walking around along the walls up against the glass plate covering the top of the terrarium

4.2.2. Experiment 2: Locomotory behaviour in large terrarium:

Of a total of five spiders, four were found to leave their retreat and explore the terrarium. Movements appeared similar to study 1; the animals were wandering about on the floor, on the sides (mainly in the corners and along the upper edge), and in rare cases even upside down on the glass plates covering the terrarium. On average they would wander around and explore the terrarium every 3.2 out of 5 nights, (Table 4.2). Out of a total of 25 nights, spiders were totally inactive in 3 nights, where they stayed inside the retreat for the entire recorded period. Inactive nights are excluded from calculations. One individual spider, (Nr.7), clearly stood out by being the only individual not found to be exploring the terrarium (Fig. 4.3), this was in contrast to its behaviour in the small terrarium were it was the most active spider.

Walking distance was found to vary from 0.1 m to 120.7 m per night. Spiders walked 35 m on average, with a median of 28.7 m, (Table 4.2).

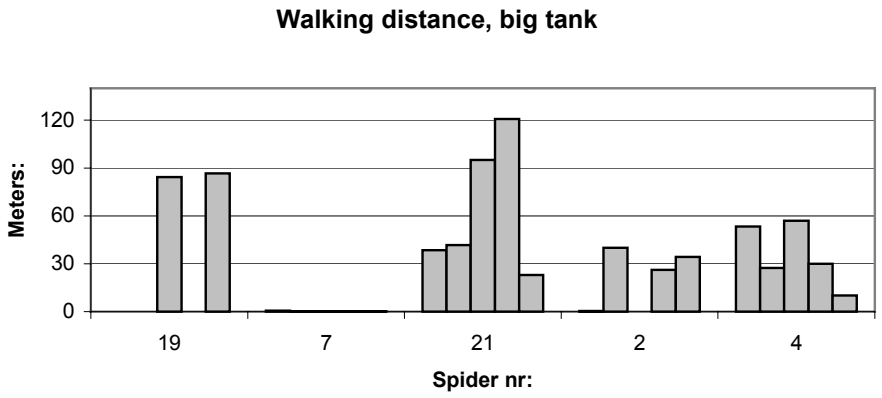
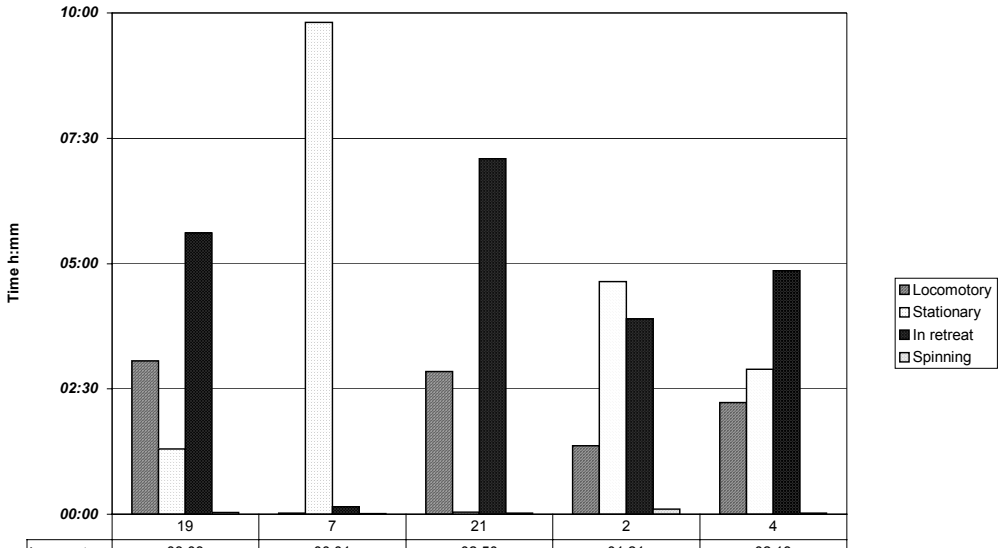


Figure 4.3: Walking distances for individual spiders, observed when studied for five nights in succession, one at a time in a large terrarium. Inactive nights included.

When examining temporal distribution between different behavioural categories (locomotory, stationary, in retreat, and spinning) results where quite similar to study 1.

There was no clear trend, and large variations both between and within individual spiders. Generally, spiders spent less time on locomotory behaviour compared to stationary behaviours and time in the retreat. All spiders spent little time spinning (Table 4.2). As with walking distance, time spent on locomotory behaviour by spider nr.7 was clearly different from the rest of the group (Fig. 4.4).

NB: It should be noted that spider Nr 7 was given a new retreat after completing Experiment 1. It then immediately blocked the entrance and moulted.



	19	7	21	2	4
Locomotory	03:03	00:01	02:50	01:21	02:13
Stationary	01:18	09:48	00:02	04:38	02:53
In retreat	05:36	00:09	07:05	03:53	04:51
Spinning	00:02	00:01	00:01	00:06	00:01

Spider nr.

Figure 4.4: Temporal distribution between behavioural categories, mean values for each individual spider as observed in large terrarium.

Table 4.2: Measures of tendencies from large terrarium, calculated from total number of active nights (n=22). (* = Calculated from all nights, n=25)

	Min	**Max**	**Mean**	**Median**
Walking distance (m)	0.1	120.7	35	28.7
Nr. of 5 nights spent exploring*	0 (Spider 7)	5	3.2	4
Locomotory behaviour (h:min)	0:00	4:57	1:44	1:54
Stationary behaviour (h:min)	0:00	10:00	4:04	2:25
Inside retreat (h:min)	0:00	8:11	4:08	4:31
Spinning (h:min)	0:00	0:12	0:02	0:01

Careful studies of the recordings and visual comparison of the spiders' walking patterns revealed no apparent search pattern, specific ambush sites, or microhabitat preference. Spiders typically followed the terrarium walls and tried to climb up the corners. Since it would require a very laborious and time-consuming process to transform the drawings of the spiders walking patterns into coordinates for computer analysis, this was not found suitable simply because it would not be likely to find any clear patterns.

4.2.3. Observations common to both studies:

- Spiders typically had only one or two locomotory active periods per night, instead of several shorter periods. They would often have three or more brief visits to their retreat during their night.

- Spiders were typically active in evenings/early nights, and often returned to the retreat towards the end of the recorded period. After finishing their active periods, the spiders would often close the retreat entrance with a curtain of silk.

- Stationary behaviour consisted almost exclusively of sitting completely still, with the body resting on the substrate. Drinking and washing only occupied a fraction of this time.

- The spiders moved around by a medium to fast walking gait, estimated at ca 15cm/sec. No spider was seen running for purely locomotory purposes.

- After most of the brief pauses observed while the spiders were out exploring (Section 3.2.1.1), a gentle shiver throughout the spider's body could be observed immediately before activity resumed.

4.2.4. Field Observations:

Seven spiders was studied 8 hours a night for a total of 36 nights. Only one spider ventured more than 15 cm from its burrow (Table 4.3), unless in pursuit of prey. This happened on only one occasion, during the wet season, where the spider walked quickly about 30 cm out from the burrow entrance, crossed left and right a couple of times, and then returned to the burrow. Unless chasing prey, all the other spiders always stayed within 15 cm from their burrow entrance on all nights studied.

Table 4.3: Results from observations of locomotory behaviour of 7 theraphosid spiders in the dry season (Oct – Nov 01) and wet season (Feb 02).

		Locomotory behaviour:				
Spider Nr	**Nights studied**	**Observed?**	**Nr Nights**	**Nr trips**	**Length**	**Duration**
1	7	No	-	-	-	-
29	8	Yes (wet season)	1	1	60 cm	1 min
35	4	No	-	-	-	-
36	5	No	-	-	-	-
37	4	No	-	-	-	-
38	4	No	-	-	-	-
40	4	No	-	-	-	-

During the first observation period, the field sites were empty and desert-like. Recent bushfires had burnt all ground cover except small tufts of burnt grasses, spread evenly throughout the area. Various sized rounded rocks (diameter typically < 20cm) where scattered about and partly embedded in a substrate of small stones and hard packed, dried out, dirt. The area provided minimal cover from predators. Based on general observations, prey availability was very low.

A number of foraging cane toads (*Bufo marinus*) were observed on almost every night. These sometimes ventured near the spider burrows, but the spiders did not retreat into the burrow even if the cane toad passed only 25 cm away. Cane toads were not seen attacking spiders, or vice versa.

During the second observation period, fresh shoots of grass provided some ground cover. Prey animal occurrence still seemed very low. Spider behaviour appeared to be unchanged.

In contrast to the lack of responses to approaching cane toads, the spiders quickly retreated if disturbed by the observer. One spider was observed to retreat into its burrow when my friend was walking more than 4 m away, though this may have been a coincidence. Very slow and soft movements seemed to be largely ignored by the spider, and were used by the observer for emergency sanitary expeditions.

Ambient light levels varied from no moon and clouded, to full moon, no clouds and starlight. There was no noticeable difference observed in spider behaviour between dark and moonlit nights. Weather conditions were generally starlight from clear sky or with some light clouds, with heavier clouds and rain only on rare occasions. A light breeze was experienced on 26 nights, with quite calm conditions on the remaining ten nights.

Temperatures generally fell by three degrees during the night. October temperatures typically started out at 25 – 26° C and dropped to 22 – 23° C, some nights were warmer. In November temperatures gradually grew higher, starting at 27 - 29° C and dropping to 25 – 27° C.

Wet season temperatures (February) were similar to late November.

One spider (*Selenotypus plumipes*) was teased from its burrow entrance to attack a straw. The spider bit onto the straw about 15 cm from the burrow, and I could drag the spider roughly 20 cm further away from its retreat, without the spider letting go. When the spider finally let go and tried to return to its retreat, it went off in the right direction, but stopped short of the retreat with roughly the same distance as I had dragged it. It then quickly probed the ground with its legs, apparently searching for the burrow entrance.

After a brief pause, it then started to walk in a slowly expanding outward spiral, in an anticlockwise direction, thereby quickly locating its retreat. This pattern has also been seen twice in the laboratory (in *Phlogiellus* sp.), when spiders have been surprised when out exploring the tank, and missed their "burrow" entrance during their retreat.

4.3. Discussion:

4.3.1. General discussion.

The first study was primarily intended to check whether or not the captive spiders would leave their retreat and wander around at night, thereby determining if it was worthwhile to go ahead with the second study.

This more elaborate study, involving a big terrarium, would provide a larger available area for the spiders to explore, and possibilities to choose between different microhabitats for ambushing or searching for prey.

When viewed in isolation from the other experiments, the results from the first study were very promising. Not only were all of the spiders found to be quite confident about leaving their retreat, but if you take into consideration that they were held in relatively small terrariums, they also walked reasonable distances (Fig. 4.1).

All spiders gave the impression of being limited in their movements by the size of the terrarium, and they were found to be able to continue exploring their terrarium for hours on end, without visible signs of exhaustion.

When spiders where introduced to the large terrarium they were found to be actively exploring their surroundings here as well. Both walking distances (Fig. 4.3), and time spent on locomotory behaviour (Table 4.1 and 4.2) increased for all spiders except spider Nr 7, which differed markedly from all other individuals.

The behaviour of spider Nr 7 may have a simple explanation: in the first study the spiders had a larger more open retreat, which was replaced with a smaller darker type, (described in Chapter 3). After I had finished recording this spider, and gave it the new retreat, it immediately covered the entrance, and moulted. In the big tank it hardly moved at all. It is therefore possible that the large walking distances observed for spider Nr 7 in the first experiment, were due to the spider not being satisfied with its retreat and looking for somewhere safe to moult. The inactivity observed in the big terrarium may be due to very low energy reserves after the moult.

As previously mentioned, all spiders were found to make frequent short pauses while walking around. This frequent transitions from rest to exercise and vice versa can

increase the total distance travelled before fatigue (Kramer and McLaughlin 2001 in Shillington and Peterson 2002). During activity, muscles in the prosoma contract and create a much higher pressure than in the opisthosoma. Brief pauses, in which the muscles are relaxed to lower the pressure, may therefore assist adequate circulation of oxygenated blood from the opisthosoma into the prosoma. This conforms well to the gentle shiver often observed immediately before activity resumes, as this could be a natural consequence of rising internal pressure.

Another option is that the animals pause to "listen in" for vibrations generated by potential prey or predators.

My personal expectation is that it is a combination of the last two factors.

During several other experiments, (Chapter 5 and 6), most spiders were also found to be exploring their surroundings. However, when given a more natural retreat consisting of a deep burrow in the ground, (Chapter 7), this roving behaviour was no longer observed. It can therefore not be excluded that locomotory behaviours observed in the laboratory were simply due to all spiders being dissatisfied with their retreats, and looking for a more suitable refuge. This may be considered a natural behaviour, since theraphosid spiders are reported to sometimes take over burrows made by other animals, e.g. the eastern pebble mound mouse *(Pseudomys patrius*) (Fred Ford pers. com.).

The results from field observations were in strong contrast to what was found in the laboratory (except from the set-up in Chapter 7). The spiders in the field were very skittish, and always returned very quickly to their retreat after chasing passing prey.

Prey density in the field, according to my observations, was very low. If this is taken into consideration together with the almost complete lack of cover left by the recent fires, conditions may have been less than favourable for the spider to venture out and search for prey. The probability of finding prey while patrolling around in the nearby area may be so low that it would not have been worth the energy spent on walking.

Spiders may in theory actively patrol the nearby area in the wet season, when tall grass would give good cover from predators, and prey densities should be expected to be higher.

Temperature in the field and laboratory were relatively similar, and hence is not relevant to explain the large discrepancy in activity level.

Although based on qualitative analysis only, I believe that spider movement in both experiments were not close to any particular pattern. Spiders seemed to follow the walls, and would often cross the floor following the large stick. They did, however, sometimes cross directly over in open spaces.

Since the retreat entrance was along the wall, it is hard to tell wether the spiders remembered where the retreat was, or if they found it again by accident.

Perhaps adult female theraphosid spiders found walking around, for example in houses, are simply spiders that have ventured too far from their refuge, and become lost. However, if found to be a well established behaviour pattern, the observed outward spiralling search pattern, used when looking for their retreat, should be sufficient to allow them to find their way back in most cases. The account of the spider dragging a chicken 50 feet back to its burrow (Chisholm 1919), suggests that they may be quite good at navigating when allowed to walk at "their own" pace. More studies on theraphosid navigation are needed.

This project clearly illustrates that it is necessary to show extreme caution in assuming that the behaviour of spiders observed in terraria are representative, or even similar, to the natural behaviour of wild animals. This is probably especially important when the spider is large compared to the terraria it is kept in, as is the case with theraphosids. When observations has to be done in laboratory conditions, observed behaviour needs to be compared with careful observations of spiders in the wild.

Temporal patterns:

Captive theraphosids could spend 4 hours or more walking at good speed, several nights in a row. This demonstrates that although they have a rather primitive respiratory system, their physiology clearly allows them to walk considerable distances if they so choose.

As expected, spiders could spend considerable time completely still. It also appeared that spiders in captivity would often not appear outside the retreat at all during the night.

The lack of observations of silken sheets or trip lines in the field was in contrast with Main's observations on *S. stirlingi* (1982), although Main did not indicate the size of the silken mesh observed around their burrows. This is discussed further in section 7.3.1.

4.3.2. Conclusion:

Due to the large discrepancy between results from laboratory and field studies, there is no foundation to claim that the roving behaviour observed in captivity (spiders leaving their retreat and exploring the surroundings for several hours) is typical for animals in the wild. It seems that Australian theraphosids that are satisfied with their retreat predominantly hunt by ambushing prey from the burrow entrance. However the study has shown that these large and heavy spiders can walk long distances several nights in a row.

Movement in captivity showed no clear pattern. Since none of the spiders observed in the field left their retreat in a similar way, it was not possible to compare walking patterns.

In captivity, the spiders tended to spend their time divided between walking around in the terrarium, and sitting in wait for prey just outside their retreat entrance. In the field, all spiders spent practically all their time sitting in wait for prey, just outside the retreat entrance. I find it highly unlikely that moving from ambush site to ambush site in the nearby area is part of the natural behaviour of Australian theraphosids.

The roaming behaviour observed in laboratory studies did not show any clear microhabitat preference for searching/ambushing for prey. Although all spiders observed in the wild only hunted from their retreat entrance, it should be noted that all retreats were close to seasonal creeks. This could be due to higher moisture levels in the ground and/or higher prey densities.

Caution is necessary in assuming that behavioural observations of captive spiders are representative to behaviour in the wild.

Chapter 5: Importance of vision in prey detection.

5.1. Introduction:

Although their eyes appear small relative to their body (pers. obs.), theraphosid eyes are actually large compared to many other spider species. Whether this is simply a function of their large size or has some behavioural significance is not known.

Considering that fossorial theraphosids are reported to sometimes roam freely (Main 1982, Shillington 2002), visual input might be more important than for many other mygalomorphs. Vision might function either as means of detecting prey or predators, or possibly be used in navigation.

Although theraphosids (like other mygalomorphs) are considered to use their vision mainly in detecting differences in light intensity (Dahl and Granada 1989), the importance of vision in prey detection has not been extensively studied.

Given their absolute size theraphosid eyes could serve important functions in prey capture even if they are only capable of detecting movements and differences in light intensity. Vision could be especially useful if the animal could detect the movement of prey too far away to be detected via prey-generated substrate-borne vibrations.

I formulated the following question.

Do theraphosid spiders use vision when they hunt, detect, and attack prey, or detect approaching predators?

Hypothesis:

H_0: Vision is poor, only used to differentiate between light and dark.

H_1: Vision is important, and aids in detecting prey and enemies.

Predictions: “Hungry” spiders should respond to nearby prey using visual cues only. This could be directly by attempting prey capture or by spending more or less time near the stimulus dependent on whether the stimulus will be interpreted as a possible prey or predator.

5.2. Results.

5.2.1. Direct observations:

No spiders responded to any visual stimulus, nor did they show other signs, like rapidly retreating, of seeing the stimulus. Even when the mouse was "jumping up and down" less than 5 cm from the spider's eyes, there was no observable response.

In the field, I did on numerous occasions "sneak up" on spiders sitting at the entrance of their retreat. There was no observable response to me slowly moving my hand about 30 cm above them, silhouetted against the sky, but they reacted immediately upon being touched, blown on, or receiving substrate-borne vibrations. When a bright light was shone on them, they would usually retreat after a short period. Similarly, when I turned the lights on in the laboratory late at night, spiders could sometimes be seen running for cover.

5.2.2. Control recordings:

There was a significant difference from the expected 1:1 ratio of turning Left / Right on number of 1st visits, ($\chi^2_c = 5.281$, $P<0.025$). Visual examination of data revealed a preference towards turning left (# left = 23, # right = 9). However, out of the difference of 14 choices towards the left, 13 where due to one single spider!

No bias appeared from analysis of total visits ($\chi^2_c = 0.128$, $P<0.75$), or total time ($t = 0.873$, $P=0.432$). Tests on 1st choice data are done on small numbers of choices, and therefore more prone to be influenced by chance than the other categories (total visits, total time). I therefore assume that the spiders show no bias towards preferring either side.

The spiders did not seem to respond to the electric fan, as there was no significant difference in 1st visits ($\chi^2_c = 2.531$, $P>0.10$), Total visits ($\chi^2_c = 0.057$, $P>0.75$) and Time use ($t = -2.015$, $P=0.114$). Any preference towards stimulus or control sides was therefore assumed not to be related to the position of the fan.

5.2.3. Responses to stimulus:

Ten meal beetles: There was a significant difference on 1st visits, ($\chi^2_c = 5.491$, ($P<0.025$). Visual examination of data revealed a preference towards the stimulus side (# Stim = 39, # ctrl = 20). However, this difference was largely due to one single spider that accounted for 16 out of the difference of 19 choices in preference for the stimulus side. No preference appeared from analysis of total visits ($\chi^2_c = 0.296$, $P>0.50$), or total time ($t = 0.271$, $P=0.8$).

Two large cockroaches: Although the cockroaches were quite active during the night, often climbing on the walls, no preference appeared from analysis of either 1st visits ($\chi^2_c = 0.028$, $P<0.90$), total visits ($\chi^2_c = 0.023$, $P<0.90$) or time use ($t = -1.026$, $P = 0.363$).

Mouse: The mouse was generally very active, digging, climbing or running around. Despite of this, no responses of any kind appeared from analysis of either 1st visits ($\chi^2_c = 0.214$, $P>0.5$), total visits ($\chi^2_c = 0.211$, $P>0.5$) or time use ($t = 0.005$, $P = 0.996$).

5.2.4. Other observations:

A "guest appearance" by a large gecko (probably *Hemidactylus frenatus*) showed me that the stimulus would be clearly visible through the glass. The gecko spent close to half an hour banging its head against the glass of the stimulus terrarium, trying to get to the meal beetles. The spider showed no response to the gecko.

5.3. Discussion:

5.3.1. General discussion:

Several aspects of theraphosid behaviour may be influenced by vision. Detection of ambient light levels is probably important to control circadian rhythms, while several visual cues may be utilised in navigation and prey detection. Unfortunately, the limited time-span of this project prevented me from exploring these categories, hence I concentrated on exploring the use of vision in prey detection.

As stated previously, I did not expect theraphosids to have acute vision, capable of detecting high-resolution images. This said, even if their eyes are only capable of detecting very crude images or movements, this may still be of importance in prey capture. Detection of visual stimuli might increase the distance upon which prey is detected, beyond the reach of the spiders' vibration-detecting senses. A rough estimate of stimulus size may also be achieved.

Theraphosids have rather large eyes compared to many spiders, and the fact that the eyes have been retained for millions of years, indicates that they do serve some function in assisting the animals' survival. In addition, the eyes are neatly arranged in a small tower on the very top of the carapace, pointing in different directions, thereby suggesting a wide field of view.

When this is taken into consideration together with the remarkable precision with which they catch their prey, the results of this study were somewhat surprising, at least for the larger stimuli.

The ten meal beetles would be relatively difficult to see, being small and dark, they were well camouflaged against the substrate, and unlike the cockroaches they were not able to climb around on the walls of the stimulus terrarium. I would therefore not expect them to be detected unless vision was quite acute, as was the case with the visiting gecko. I included the meal beetles in this experiment to possibly get a rough idea of how big the visual stimulus had to be in order to be detected, if I had found that e.g. the cockroaches would be detected and the meal beetles not.

At first glance the significant difference found on number of 1st visits, with meal beetles as the stimulus, seemed promising. However, closer inspection of data revealed that this was largely due to one single spider. Number of 1st visits were generally low, mostly between 0 and 4 on either side. I therefore feel that tests run on 1st visits could be highly influenced by chance. I would have higher confidence in significant results from the other tests, done on total number of visits, and total time spent on each side. In the case of meal-beetles no further significance was found.

The other two, much larger stimuli should have been easier to detect. The cockroaches would often walk on the wall of the stimulus terrarium, facing the "arena" and the mouse would often stand up against the wall. This way the stimuli would often move less than 5 cm from the spider's eyes. Despite of this, no significant difference was found on any of the selected criteria. If anything, the results was "significantly insignificant" with P values reaching 0.996 for the t-test run on total time spent near and far from the mouse.

It should be noted that the experimental set-up worked adequately, stimulus animals were active during the night, and most spiders came out of their retreat and visited one or more of the sides of the arena. Even in two cases where the spider only came half way out of the retreat, the visual stimulus would move within 17 cm of the spider's eyes. If visual cues were important in prey capture, this should have triggered a response, especially from the largest stimulus (the mouse).

Careful examination of the data revealed no clear difference between the behaviour of the single *Selenotypus plumipes* compared to the four *Phlogiellus* sp. used in the experiment.

It is of course a theoretical possibility that the spiders did actually see the stimulus, but chose to ignore them, for unknown reasons. I find this highly unlikely since theraphosids most often are opportunistic feeders, willing to investigate anything that's moving near by as a potential prey.

This study therefore indicates that vision is not important in detection of prey in Australian ground-dwelling theraphosids of the genera *Phlogiellus* and probably also *Selenotypus*. Although one needs to be very careful with generalising what is found for one species to be valid for other species and even other genera, I expect that the results

of this study are representative for most theraphosid genera. This opinion is based on the relatively similar external morphology of the eyes of theraphosids, and similarities in prey capture behaviour among all the different species I have kept in captivity during the last decade (*Lasiodora, Brachypelma, Theraphosa, Grammostola, Pterochilus, Chromatopelma, Selenocosmia, Phlogiellus, Selenotypus* etc.)

Although not recommended (based on the results of this study) anyone wishing to do further studies would be advised to look at arboreal species, believed to be active during the day, as vision might be more important for these animals.

It is possible that theraphosid vision may detect very large approaching objects, like a walking human. More likely, vision may be utilised for navigation e.g. when returning to their burrow after chasing prey. The well known story of the spider dragging a chicken 50 feet back to its burrow (Chisholm 1919), suggests that theraphosids may have well-developed means of navigation. This however is a field awaiting further studies.

Although spiders in the lab were sometimes seen to be active during the day, most spiders both in the lab and in the field normally did not emerge from their retreats until dusk. This supports the general belief that vision is important in determining ambient light levels, influencing when the spider chooses to be active. Considering the results from this study, favoured light levels for active periods are probably not related to visual detection of prey, but rather to lower predation risk from visually oriented predators, while the spider is exposed.

Only relatively straightforward statistical methods were used to analyse data, and it could be argued that additional analysis is necessary. However, when dealing with such a small sample size (n = 5), it is my belief that any trends strong enough to allow me to confidently reject the null hypothesis should have emerged from the analyses performed.

After looking through more than 320 hours of videotapes, and observing the spiders for countless hours both in the field and in the laboratory, I have never seen any clear behavioural responses to visual stimuli, except to changes in ambient light level.

5.3.2. Conclusion:

This study indicates that vision is not important for detection of prey by Australian theraphosids of the genus *Phlogiellus* and probably also for *Selenotypus*. These results may be representative for other Australian genera, and many overseas genera as well.

Although vision probably is unimportant in prey detection, the eyes seem to detect ambient light levels, and hence are important for control of circadian rhythms.

It is possible that vision is actively used in navigation, but this is a field currently awaiting studies.

Chapter 6: Importance of chemical senses in prey detection.

6.1. Introduction:

The importance of chemical cues in prey detection by theraphosids (or any spider) is still mostly unknown. Spiders respond to chemical cues from conspecifics, indicating that their chemical senses may be well developed (Chapter 2). Considering this, it seems possible that theraphosids may respond to chemical cues from nearby prey.

Since theraphosids are sometimes encountered roaming freely (Main 1982, Shillington 2002), chemical stimulus may be more important for theraphosids than for many other mygalomorphs that only hunt in the immediate proximity to the burrow. For free-roaming theraphosids, any ability to sense chemical cues from potential prey could be useful for prey localisation.

Compared to all other spiders, the shear size and brute strength of theraphosids also puts them in the unique position of being able to prey on small mammals (e.g. mice) with ease (pers. obs.). Any ability among theraphosids to detect chemical cues from mammals could therefore serve pure predatory purposes, whereas in other spider families its function would probably be more limited to anti-predatory behaviours.

I formulated two questions.

1. **What role do chemical senses have in recognising prey or enemies?**

Hypotheses:

H_0: Chemical senses are not important in detecting prey / predators.

H_1: Chemical senses are important in detecting prey / predators.

Predictions: Tasty immobile food items (e.g. raw meat) should be taken. Spiders should respond to scent trails from prey previously allowed to walk on the substrate.

2. Is it necessary to touch the item, or are airborne odours recognised?

Hypotheses:

> H_0: Chemical stimuli are detected by taste only (contact), and olfactory cues cannot be detected in air currents (no contact).
>
> H_1: Chemical stimuli can be detected in air currents.

Predictions: Spiders should locate smelly immobile food items they cannot touch and react to airborne odours from prey / predators.

6.2. Results:

6.2.1. Experiment 1: Dead food items.

Uncovered pieces of raw meat were located and eaten by 6 out of 10 spiders, (Figure 6.1). Covered pieces were not located and / or were ignored by all spiders.

6.2.2. Experiment 2: Substrate-related chemical cues.

Although preliminary studies seemed promising, very few spiders entered the 2-way labyrinth during the experiment phase. With crickets, six spiders did not enter the labyrinth at all, two spiders went to the stimulus side only, one to the control side only, and one first to the stimulus and then to the control side. None of the spiders entered the labyrinth with a mouse as stimulus, see Figure 6.1.

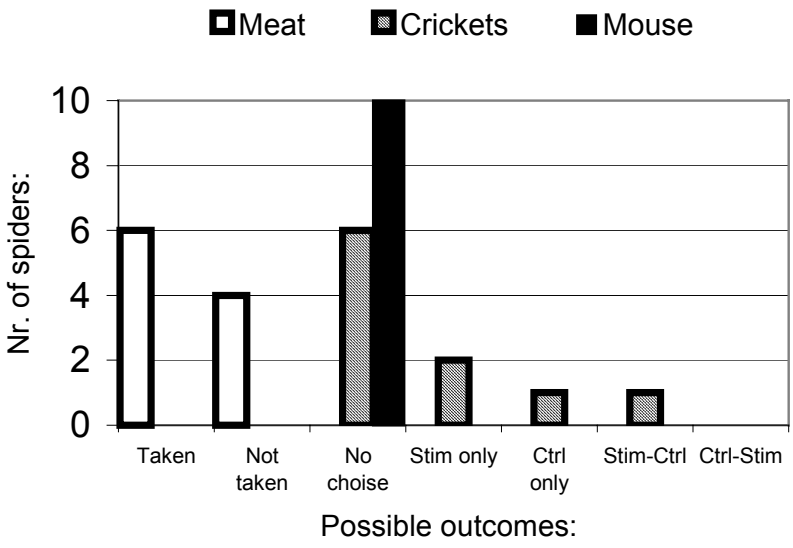


Figure 6.1: Results, contact chemoreception: (covered meat-pieces were ignored by all spiders and are not shown in table).

6.2.3. Experiment 3: Olfactory stimulus

Control recordings:

There was a significant difference from the expected 1:1 ratio of turning Left / Right on 1st visits, (χ^2_c = 9.796, P<0.005). Visual examination of data revealed a preference towards turning right (# right = 39, # left = 15).

No bias appeared from analysis of total visits (χ^2_c = 1.906, P>0.10), or total time (t = 1.523, P=0.202). Tests on 1st choice data are done on a small number of choices, and therefore are more prone to be influenced by chance than the other categories (total visits, total time). I therefore assume that the spiders show no bias towards preferring either side.

6.2.4. Responses to stimulus:

Meat: No significant response:

There was no significant difference on 1st visits, (χ^2_c = 1.439, P<0.1),
and no preference appeared from analysis of total visits (χ^2_c = 1.232, P>0,25),
or total time (t = 0.661, P=0.545).

Cockroaches: No significant response:

Again, no preference appeared from analysis of either 1st visits (χ^2_c = 0.0 P<0.999), total visits (χ^2_c = 0.126, P<0.75) or time use (t = -0.577, P = 0.595).

Mouse: No significant response:

Like above, no preferences appeared from analysis of either 1st visits (χ^2_c = 0.214, P>0.5), total visits (χ^2_c = 0.211, P>0.5) or time use (t = 0.005, P = 0.996).

Spider: No clear response:

There was a significant difference from the expected 1:1 ratio of turning Left / Right on 1st visits, (χ^2_c = 6.469 P<0.01). Visual examination of data revealed a preference towards turning towards the right (# right = 80, # left = 50). However, no bias appeared

from analysis of either total visits ($\chi^2_c = 0.435$, P>0.50), or total time (t = 0.599, P=0.582).

6.3. Discussion:

6.3.1. General discussion:

The fact that all spiders have numerous and well-developed sensors for detecting various chemical stimuli strongly suggests that chemical stimuli serve various functions important for spider survival. In the case of theraphosids these functions are still mostly unknown, and few of them have been investigated scientifically.

Chemical stimuli could in theory be used by spiders in several ways, like finding mates or serving various functions in prey detection / predatory behaviour. In special cases chemical stimuli, e.g. olfactory cues, may even enable the animal to detect environmental hazards like an approaching fire. This study concentrated on the use of chemical senses in detecting nearby, already dead, food items and the presence of live potential prey or predators.

As mentioned earlier (Chapter 2) , chemical stimuli do not give the predator information of a kind that serves to pinpoint prey location for the final strike. Instead chemical stimuli may be expected to influence general predatory behaviour, e.g. by encouraging spiders to spend more time ambushing or searching for prey, or in the case of potential predators, eliciting defensive behaviours or inducing flight.

6.3.2. Dead food items:

I first wanted to see if chemical stimulus only would be sufficient to make a theraphosid spider detect, grab, and eat a food item, or whether vibrational cues are necessary. The fact that 6 out of 10 spiders picked up and ate the piece of meat clearly shows that the spiders can taste, and recognize, food items that are not moving. This opens up the theoretical possibility of these spiders feeding on carrion in the wild, but I don't think this would happen often, considering that the spiders are primarily ambush predators, hunting from the burrow entrance (Chapter 4).

To explore in more detail whether the spiders used "taste" or "smell" to find the meat, I repeated the experiment, but covered the meat under a perforated piece of paper. This time none of the spiders found the meat, suggesting that the spiders could not smell it,

but found it when they accidentally touched and tasted the meat with their legs, while exploring their terrarium.

However, it was possible that only very limited "smell" escaped through the paper, and the meat was therefore included as stimulus in the olfactometer experiment.

6.3.3. Substrate-related chemical cues:

On a hypothetical hunting expedition, it should be highly useful for the spiders to be able to respond to substrate-related scent trails, as this would assist prey location. Even when ambushing for prey from the burrow entrance, substrate-related scent trails could influence how long the spider chooses to wait for prey, or even induce short "searching expeditions". The results of the two-way labyrinth experiments where therefore slightly disappointing compared to the results from the first experiment. That none of the spiders entered the labyrinth following the "mouse-trail" could mean that they recognized it as a potential predator, and hence avoided the labyrinth. However, considering the size and strength of the spiders used in the experiment, I think this is unlikely.

Only 4 of 10 spiders entered the labyrinth with crickets as the stimulus, and there was no uniform preference towards the stimulus side.

As a whole, this experiment therefore does not indicate that substrate-related scent trails from prey are important in theraphosid predatory behaviour.

It is possible that the spiders did in fact increase the time they spent ambushing from their burrow entrance on experimental nights, but this was not tested. Some spiders were seen exploring their terrarium or sitting with legs touching the labyrinth substrate, without entering the labyrinth. This again indicates that the substrate-related chemical stimulus was not detected.

6.3.4. Olfactory stimulus.

In this experiment getting even a very limited number of replicates (n = 5) proved very time consuming, due to varying "cooperativeness" among the experimental spiders.

An experimental recording was considered successful if the spider, at its own pace, left its retreat and started exploring the Y-maze. However, spiders were often content staying the whole night just in the holding area or not emerging from the retreat at all. I therefore had to record close to 70 nights to get the 45 successful ones used for data analysis.

At one occasion the mouse chewed through its fenced-off area during the night, and since it could then have touched the air-intake cylinder and provided vibrational cues for the spider, the night had to be cancelled and re-recorded.

When determining the types of stimulus for this experiment I chose meat-pieces as a follow up to the first experiment, another spider as a potential predator, cockroaches as potential prey and a mouse that could be both predator and prey. All these stimuli could theoretically be encountered by the spiders in the wild.

Even though meat was found to be readily accepted as food and eaten, there was no response to this stimulus in the olfactometer set-up. This was an expected result consistent with the first experiment and indicates that olfactory stimulus from meat does not elicit a predatory response in Australian theraphosids.

The lack of response to the smell of cockroaches was somewhat more surprising as these prey animals, would be a normal prey relatively frequently encountered in the wild. In the experiment I used domestic cockroaches (*Periplaneta americana*) and it is possible that I would have obtained different results had I used native species as stimuli.

If a theraphosid out on a hunting "expedition" encounters the burrow of another theraphosid, it should be of great advantage for the approaching spider to smell that the burrow is inhabited, so as to avoid a confrontation. This ability has been observed in male theraphosids seeking the burrow of nearby females (Chapter 2). The lack of any clear response to the theraphosid spider as a stimulus in this experiment, indicates that the males mentioned above probably reacted to sex-pheromones from the female and

not the “spider smell” associated with any theraphosid and its webbing. It is possible that substrate-related cues from other theraphosids would have elicited an response, but this awaits further studies.

The stimulus I expected most likely to give a clear response was the mouse. As native mammals were not available, a domestic mouse was used in the experiment. I expected the smell to be similar enough to wild animals as to elicit any natural behavioural responses (e.g. snakes respond readily to smell from domestic mice) but this can be debated.

Since there was no detected response to the mouse odour I expect that theraphosids do not detect and / or respond to this type of stimulus in the wild.

As a whole, the olfactometer experiments therefore indicated that olfactory stimuli are not detected and used in theraphosid predatory behaviour.

Only relatively straightforward statistical methods were used to analyse the data, and it could be argued that additional analysis may be necessary. However, with such a limited number of replicates, I feel that any trend strong enough to allow me to reject the null hypothesis with confidence, should have emerged.

6.3.5. Conclusion:

It has been found that theraphosid spiders can detect and readily pick up and eat already dead food items, like pieces of meat.

Substrate-related scent trails from potential prey animals failed to elicit any response, and are probably not detected and / or not used in predatory behaviour.

Olfactory stimuli appear not to be important for detection of prey by Australian theraphosids of the genera *Phlogiellus* and probably also *Selenocosmia*.

Chapter 7: Function of vibration detecting senses in prey detection.

7.1. Introduction:

In the context of predatory behaviour, vibrations have tremendous importance as most spider species use detection of prey-generated vibrations, through various media, as their primary means of detecting prey (Barth 1985, Foelix 1985).

A predator detecting vibrations from a nearby source may theoretically be concerned with two "questions": "Where?" and "What?" is the source. While hunting the spider has to decide whether to ignore a stimulus, investigate it closer, attack it, retreat, or respond with other behaviours like threat displays. Considering that theraphosids are ancient creatures, it seems reasonable to expect that they, like araneomorph spiders, have developed very sensitive sensory systems for detecting vibrations, and are capable of some discrimination between vibratory signals from potential prey, as opposed to signals from abiotic elements (a falling stick or leaf) and "background noise" (wind, running water).

Prey capture responses towards a non-prey stimulus are possibly costly for the spider both in terms of energy efficiency and exposure to predators. Since during the dry season Australian theraphosids are often faced with long periods of low food availability and at this time they are easily seen in barren post-burn habitats, "wasted" responses should be avoided to maximise energy efficiency and survival.

Very little scientific knowledge exists about how various vibratory signals influence and are used in theraphosid predatory behaviour. I have chosen three questions to explore in some detail:

1. How accurately can the spider determine the position of an animal sending out vibrations of different frequencies and intensities?

- H_0: The spider can only detect that a vibration source is present, but not its position.
- H_1: The spider can detect the position of the vibrational source.

Prediction: Prey capture responses should be accurate when prey is within striking distance.

2. Can the spiders recognize abiotic sources and different prey / enemy organisms from the vibrations they are sending out?

- H_0: The spiders can only detect that there is something moving, not what it is.
- H_1: The spider can differentiate between abiotic factors and the vibrations sent out by different animals.

Prediction: Spiders should vary their response to vibratory signals generated by prey and non-prey items.

3. Does the spider use silk and / or other items to aid detection of vibrations.

- H_0: The spider does not use silk and / or sticks etc. to aid detection of vibrations.
- H_1: The spider uses silk and / or sticks etc. to aid detection of vibrations.

Predictions: Silken trip-lines / sheets should be found both in captivity and the wild, and positively affect prey detection distance and capture.

7.2. Results:

7.2.1. Experiment 1: Accuracy of spider responses to vibratory stimulus.

With crickets as stimulus I got 43 responses from a total of 5 spiders, but the number of responses per spider varied greatly. Responses suitable for measurements are shown in Table 7.1.

With cockroaches as stimulus I got 20 responses from a total of 3 spiders. Six of these responses were from cockroaches climbing on a leaf (see section 7.2.3.). Most of the remaining responses to cockroaches were "half-hearted" and often delayed in time. Because of this, the exploratory analysis below is based on responses to cricket prey only.

It should be noted that apparent "trends" presented below are based on limited data.

A. Detection distance and angle - response type:

Mean prey-detection distances for prey capture (PC) and prey capture response (PCR) responses were quite similar and considerably smaller than the prey capture movement (PCM) mean (Fig 7.1).

PC and PCR responses may be considered the same type of response, but with a different outcome. Considering mean detection angles, detection angle does not appear to influence the type of response (Fig 7.2).

Table 7.1: Spider responses to cricket prey, PC = prey capture, PCR = prey capture response and PCM = prey capture movement.

Spider:	Rsp.type:	Nr.Rsp.:	Detection distance (cm) :			Detection angle (degrees) :		
			Max.	Min.	Mean ± SD	Max.	Min.	Mean ± SD
19	PC	3	8.8	1.2	4.1± 4,1	149.2	10.7	77.3 ± 69,4
	PCR	10	15.8	0.9	5.2 ± 4,7	178	4	74.9 ± 53,1
	PCM	9	20.3	1.4	10 ± 6,1	179.7	9.3	72.5 ± 55,3
30	PC	2	2.7	2	2.4 ± 0,5	92.7	91.4	92,1 ± 0,9
	PCR	1	2.3	2.3	2.3	39.9	39.9	39.9
	PCM	1	11.8	11.8	11.8	69.9	69.9	69.9
31	PC	1	1.7	1.7	1.7	4	4	4
	PCR	1	1	1	1	94.7	94.7	94.7
33	PC	3	3.1	0.6	2.2 ± 1,4	93	59.9	73.9 ± 17,1
	PCR	2	6	2.5	4.3 ± 2,5	136	54.9	95.5 ± 57,3
	PCM	2	4.1	3	3.6 ± 0,8	79.5	84.6	82,1 ± 3,6
42	PC	2	3.7	3.3	3.5 ± 0,3	117.3	42.3	79.8 ± 53
	PCR	3	4.4	1.9	2.8 ± 1,4	108.5	49	77.9 ± 29,8
	PCM	3	26.2	12.2	17.5 ± 7,6	79.1	50.2	61.8 ± 15,3
Total:					Mean of Means ± SD			Mean of Means ± SD
	PC	11	8.8	0.6	2.8 ± 1	149.2	4	65.4 ± 35
	PCR	17	15.8	0.9	3.1 ± 1,7	178	4	76.6 ± 22,6
	PCM	15	26.2	1.4	10.7 ± 5,7	179.7	9.3	71.6 ± 8,3

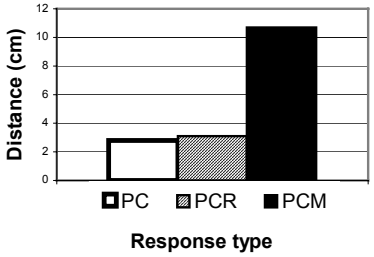


Figure 7.1: Mean detection distances for each response type.

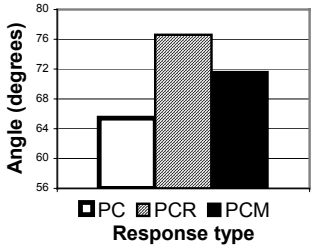


Figure 7.2: Mean detection angles for each response type.

Plotting detection angle and detection distance, for each individual measurement in all response categories on the same graph (Fig 7.3) gives an overview of all responses to cricket stimulus. Very few PCRs and PCs are initiated at detection distances longer than 10 cm.

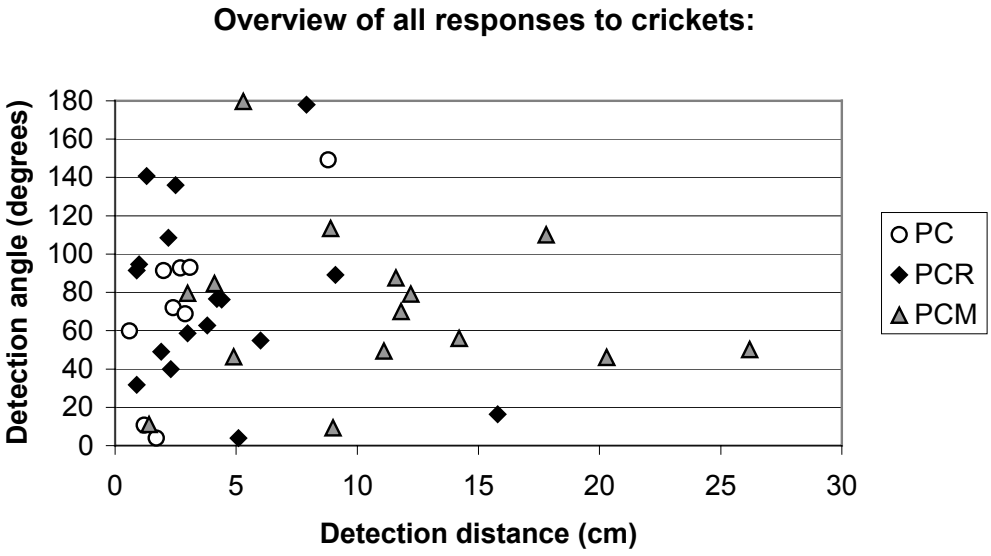


Figure 7.3: Overview of responses to crickets as vibratory stimulus, PC = prey capture, PCR = prey capture response and PCM = prey capture movement

B. Detection distance - Rest distance.

Rest-distance, is the distance between the base of the spider's chelicera and the position of prey at time of detection, after the spider's initial lunge. The measurements are from PC and PCR responses only. Rest-distances when prey position was under the spider's prosoma was set to 0.

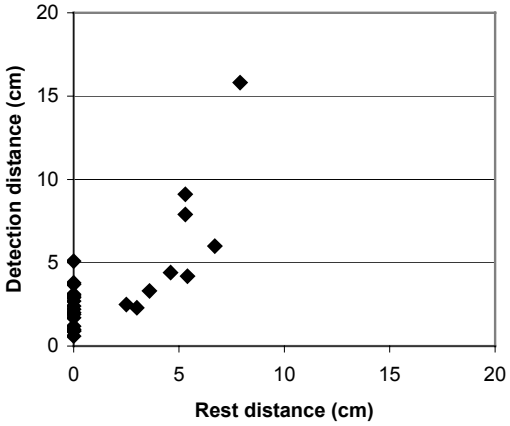


Figure 7.4: Remaining distance to prey position at time of detection, for various detection distances, after initial strike. PC and PCR responses only.
Rest-distances where the prey position ended up under the spider's prosoma were set to 0.

As detection distance increased, so did the rest distance, indicating that spiders got less precise at detecting prey distance as distance to prey increased (Fig 7.4).

However, the accuracy of spider's detection of prey distances seems independent of detection angle (Fig 7.5).

C. Detection angle - Rest angle.

Rest angle indicates how well the spider aligns itself towards the position of the prey when it was detected. When the spider's initial response was so good that the prey position was well inside the spider's legs, rest angle was set to 0 as discussed in section 3.2.4.2.

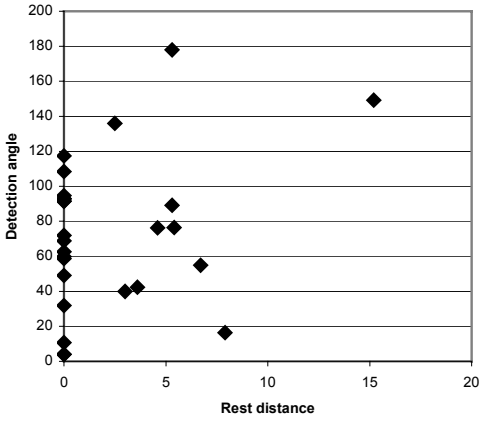


Figure 7.5: Remaining distance after the initial strike, to prey position at time of detection, for various detection angles. PC and PCR responses only. Rest distances where the prey position ended up under the spiders prosoma was set to 0.

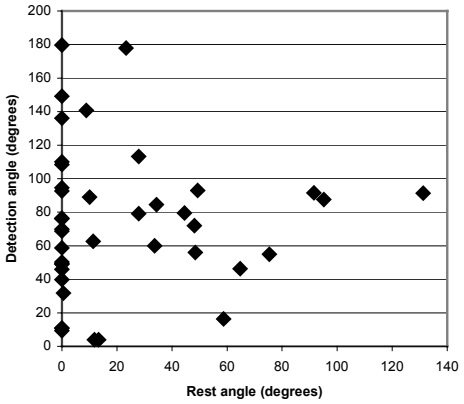


Figure 7.6: Rest angle after the initial strike, from direct frontal alignment of the spider, towards the position of prey at time of detection, for various detection angles. PC, PCR and PCM responses included. Rest angles where the prey position ended up inside the spiders legs, was set to 0.

Field observations:

Spiders in the field were more "on the edge" and eager to race out after all nearby prey. Only four responses were observed, but here detection distances varied from roughly 10 to 40 cm. A lightning fast successful attack on a wolf spider (Lycosidae), about 25 cm from the spider, and a quick race after a cricket 40 cm away, were clearly different from laboratory observations. Responses in the field were always "full force - full speed" whereas laboratory responses were sometimes "half-hearted" and nearby prey were often ignored.

Other observations:

- The capture process is dynamic. After the initial strike there are often several re-orientations as the prey reacts with avoidance behaviour.

- Spiders appear to be able to continuously detect the direction of prey movements, simultaneously with walking / running themselves.

- Fangs were seldom used in a simple "pick - axe" fashion, where the spider spears its prey with a downward fang motion. Typically, prey animals were grasped with the front legs, manipulated and "scooped in" towards the fangs and bitten (Fig 7.7). When biting prey, the chelicera were typically held at an angle (estimated 60 - 70 degrees) to each other, enabling spiders to "gape wider" than if the fangs had moved on parallel axes (Fig 7.8).

Figure 7.7: "Scooping motion" using legs to grab and manipulate prey towards chelicera, for fang insertion.

Figure 7.8: Angled chelicera, typically held at 60 - 70 degrees (estimate).

- When attacking prey, front legs were often lifted up high, and slammed downwards and forwards. In one instance, a spider slammed its legs onto a falling leaf that had landed on the edge, before retreating quickly. This may indicate that the point of first contact may be used to estimate prey size.

- Crickets seemed to be detected much more easily than even large cockroaches. Nearby crickets nearly always triggered a response, whereas cockroaches could walk past and even touch the spider with their antenna without any response from the spider.

7.2.2. Experiment 2: Responses to various "vibrational signatures".

Leaves and sticks:

Four spiders were tested four times with each stimulus, except for one spider that was only tested twice with each of a large and small falling stick. "Soft" landings of leaves tended to initiate prey capture responses, whereas "hard" landings of sticks were largely ignored. Spider responses are shown in Figure 7.9.

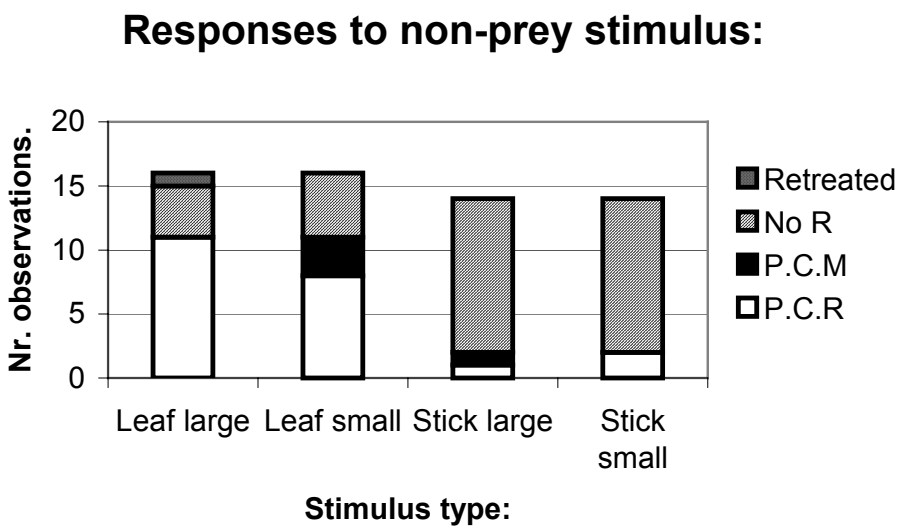


Figure 7.9: Responses to various abiotic stimuli, falling onto the ground. PCM = prey capture movement, PCR prey capture response.

Rattling leaf:

A leaf rattling in the "wind" from a small computer fan was either ignored, or (most often) caused the spiders to retreat to their burrow shortly after I started the fan. This was in contrast with field observations, where spiders ignored even moderately strong winds and stayed put, waiting for prey at the burrow entrance.

7.2.3. Experiment 3: Is detection of vibrations aided by silk or other items?

Silken sheets / trip-lines:

In the "hole in the ground set-up" 2 out of 5 spiders constructed small silken sheets around the burrow entrance (r = 6 - 7 cm). Available prey capture data were insufficient to determine importance in prey detection.

However, when spiders were waiting for prey, they often waited with their legs stretched out beyond the reach of the silken sheet.

In the field silken trip lines or sheets were not observed, however a small fringe of silk radiating 1 - 2 cm from the burrow was spotted on a few occasions. As described above the spiders normally extended their feet beyond the silk when waiting for prey.

In their keeping containers, spiders normally covered the floor with a layer of silk. Similar behaviour was observed once in the field, when a spider inhabiting a large tunnel (r ~ 10cm) had covered the floor with a similar layer of silk. The silken sheet did not extend beyond the tunnel opening.

Other items:

No spider was observed to arrange nearby sticks etc. in a manner as to aid detection of passing prey. However, in the “hole in the ground set-up” cockroaches were detected when climbing on top of a leaf lying on the ground, but ignored when walking directly on the substrate (see above).

Raw-data for all analysed responses are available in Appendix A4.

7.3. Discussion:

7.3.1. General discussion:

The experimental set-up worked satisfactorily, but it proved much harder than expected to get the necessary data. This was due mainly to a large discrepancy between behaviour of spiders held in the laboratory, and in the wild. In the field spiders nearly always spent most of the night waiting for prey at the burrow entrance, whereas in the "hole in the ground set-up" spiders could be totally inactive for 4 - 7 days. When emerging from their retreat, captive spiders also seemed less eager to catch prey than spiders in the field. None of the spiders used in the experiment had been fed recently, and the small relative size of their abdomen did not indicate high energy reserves. I have also observed this variation in eagerness to catch prey in my pet theraphosids, although they were all kept under near identical conditions. Naturally, hunger levels, frequency and regularity of prey availability and hydration levels, may influence this behaviour. Decreasing food and water availability a few months prior to the experiment may have resulted in more "field like" behaviour.

However, spiders in the "hole in the ground set-up" were similar to spiders in the field in that they did not leave their retreat to walk around and explore their surroundings.

Due to the limited data, I consider the results to indicate trends and possible patterns, rather than firmly establish them. However, some trends are clear and I would expect them to be confirmed by additional data.

Like most spiders, theraphosids use vibrations as their primary means of detecting prey. In contrast to their visual and olfactory senses, they appear to have a very sensitive and well-developed system to detect vibrations. In the "hole in the ground set-up", a cricket was detected while walking on compact dried dirt, at least 26 cm away (Table 7.1) and in the field, a spider was seen charging after a cricket that was walking more than 40 cm away.

Theoretically, a spider should not strike at nearby prey without knowing both direction and distance, simply because a "blind strike" most likely is a waste of energy. On the other hand, a "blind strike" (low chance of prey capture) may be better than no

predatory response (no chance of prey capture) if prey availability is low. All PC and PCR responses were initiated at detection distances less than 16 cm, most of them less than 10 cm (Fig 7.4). PCM responses, however, were initiated at distances of more than 26 cm, the spider turning correctly towards the prey. This indicates that the spiders cannot accurately detect the distance to stimuli more than 10 - 15 cm away, but that direction can probably be detected at much larger distances. These results (although based on limited data) are notably similar to the patterns Brownell (1977,1984) found when studying sand scorpions (*Paruroctonus mesaensis*).

Detection angle did not appear to influence type of predatory response, i.e. the spiders attacked prey approaching from all angles, (in front, to the side, and to the rear) as long as the stimulus was close by (Figure 7.3).

It also appears that the direction of the incoming stimulus does not influence how well the spiders detect distance and angle to the prey (Fig 7.5 - 7.6). Considering the near circular arrangement of vibration detecting sensors (on each leg), this is as expected.

More surprisingly, the spiders seemed equally good at successfully capturing prey, through all detection angles (Fig 7.3). I strongly suspect this to be due to my limited data, since prey to the rear of the spider should have a higher chance of escaping, since the spiders need to spend some extra time turning around.

When watching theraphosids catch prey in real-time, it appears as if they simply throw themselves on top of the prey and spear it so quickly that the prey has no time to react. However, when studying prey capture in slow-motion, one clearly sees that this is not the case. The prey animals normally react extremely quickly, and try to flee, causing the spider to run after them. It appears that the spiders can follow running prey without stopping to "listen-in" on the vibrations.

When catching up with the prey, there follows a sometimes lengthy process of grappling and fighting with the prey before it is successfully brought in towards the fangs and bitten. During this process spiders typically maintain contact with the substrate by the 4^{th} pair of legs, while the palps, 1^{st}, 2^{nd} and 3^{rd} pair is used for manipulating prey. When struggling with larger prey, like a big beetle, the 4^{th} pair of legs are also applied.

Fangs appear to be used in a somewhat pincer-like fashion, rather than spearing the prey like a "pick-axe". Instead of spearing prey between its fangs and the ground, the prey are held in a firm grip by the legs (see above) until the fangs have got a good hold of the prey. Soft-bodied prey like crickets are simply squashed between the fangs and the chelicera, while upon encountering hard-bodied prey, the spider "walks" its fangs over the prey seeking vulnerable spots for fang insertion.

If the prey is struggling after being bitten, the spider often stands high and wide on its legs. Holding the prey in the fangs only, it balances on some legs while bending the other legs (including palps) away from the prey, changing which legs it stands on according to which legs are being touched by the prey. If the prey is large, the spider might even roll on to its side and bend all its legs and palps back over its prosoma and away from the prey, holding on to the prey with the fangs only, until the venom takes effect. Fangs are typically held at an angle to each other and the spiders often hang on to the prey with one fang only while searching for a new grip with the other, prey manipulation sometimes being assisted by the palps and legs (seemingly when the fangs need a better grip). The prey capture process, from detection to killing of various prey, is complex and in need of further studies. Several informal reports (Chapter 2) indicate that small mammals (mice) are always grasped in the neck, dying shortly thereafter.

Considering the possibilities of different "vibrational signatures" made by various prey, even from my limited number of observations it seems clear that cockroaches are able to, to a certain degree, avoid detection by the spiders, whereas crickets and beetles are more easily detected.

With the abiotic stimuli, the spiders appear to recognize differences in "vibrational signature" and vary their behavioural response accordingly.

The fact that the "rattling leaf" was never attacked also indicates that theraphosids do not simply lunge after anything that moves, but seem to interpret vibrational signals in a more complex manner making this another field worthy of further studies.

It would be particularly interesting to explore if the spiders can learn to recognize the "vibrational signature" from unwanted prey or prey too large to overpower (e.g. large beetles, echidnas (*Tachyglossus aculeatus*) and dogs. This was what I had in mind when offering a heavily armoured beetle to spiders in the "hole in the ground" set up, but

sadly the beetle died (of old age) and I was not able to find a replacement within my time limits for this experiment.

The construction of a mesh of web around the burrow was reported by Main (1982) and also constructed by some captive spiders during this study. However, according to my field observations of some Australian theraphosids they do not appear to construct trip-lines in the wild, although there might be some silk radiating 1 - 2 cm from the burrow entrance. The importance of such sheets in aiding prey detection seems debatable, since when the spiders were ambushing for prey they often extended their legs beyond the reach of the silken sheet. Why the sheet of silk was not extended could be due to a number of reasons:

Firstly, it could be that prey generated vibrations do not travel that much further along a slack silken trip line or sheet lying on the ground, than through the body of the substrate itself. In the field, prey was detected over 40 cm away through the ground, theoretically giving theraphosids a large circle (d = 80 cm) in which they will detect passing prey. In most cases this area would probably be sufficient. Trip lines should be easier to construct, and if tightened a bit, they should effectively transport vibrations over considerable distances. I have never seen a theraphosid either making or tightening a long line in this manner.

Secondly, construction of a large silken sheet would be costly in terms of energy and would be in need of frequent repairs. In hostile areas with low prey availability, like dry Australian bushlands, silken sheets may not increase the amount of prey captured sufficiently to be worthwhile energy-wise. These conditions, however, do not apply to the many rainforest-dwelling species.

Thirdly, theraphosids are believed by some to leave their burrow in search of prey. Although this behaviour is not supported by this study (Chapter 4), any such frequent exploratory behaviour would render a silken sheet around the burrow of very limited use.

7.3.2. Conclusion:

Although based on limited data, these experiments revealed some clear trends.

The detection angle of vibrational stimulus seems to have little influence over type and precision of the predatory response.

Detection of distance to the vibrational source appears to become less precise as the distance increases, and in captivity very few prey capture responses are initiated at prey distances more than ca 10 cm.

The prey capture process is dynamic, often including several re-orientations towards fleeing prey, and manipulation of prey by the legs and pedipalps, to manoeuvre it into position for biting it.

There is a strong indication that theraphosid spiders can vary their response, according to various “signatures” of abiotic and biotic vibratory stimulus.

There is no evidence for large silken sheets or “trip-lines” being constructed as means of aiding prey detection, under normal conditions. Silk around entrances may serve to stabilize particles but are probably not relevant in prey detection.

Chapter 8: 3D detection of prey stimulus position.

8.1. Introduction:

The idea of this experiment started overseas years ago, from a behavioural observation of one of my pet tarantulas (*Grammostola spatulata*). It had been resting for hours when it suddenly walked quickly approximately 20 cm towards the other end of the terrarium, immediately started digging, and captured a burrowing mealworm at a few cm depth. I was intrigued by the fact that the spider didn't spend any time searching for the prey on the surface, but seemed to know that the prey was below surface level. The substrate in the terrarium was a light but hard and coarse "sand-like" material (a type of "cat-sand") not unlike the coarse sand found in dried creeks.

Theraphosids are large and strong enough to easily dig down a few centimetres in relatively loose substrates (sand, moist dirt) and one can imagine theraphosids digging to get to prey animals that have made a temporary escape underneath a small rock. I have seen this in captive theraphosids of different species and from many continents, (eg. *Grammostola spatulata* (Chile)*, Pterochilinus murinus* (Tanzania)*, Brachypelma albopilosa* (Mexico). Since theraphosids from different continents display similar digging responses this behaviour may be of ancient origin.

Upon encountering subsurface prey, the spider should avoid trying to dig out prey that are burrowing too deep for easy capture. It seems safe to assume that the deeper a prey animal is burrowing the longer it will take to dig it out. Some burrowing animals respond to disturbances from above by burrowing deeper (Brownell and Farley 1979), thus for an attack to succeed, the prey must be dug out quickly, before the prey goes too deep in the substrate.

In large areas of Australian bush lands, the ground is very hard and compact during the dry season. This creates difficult conditions for rapid digging (pers. obs.). Considering that the spiders normally forage from the burrow entrance (Chapter 4) it appears as though they might rarely come across sub-surface prey in this manner. However, even in these habitats loose substrates can be found in the bottom of small rivers and creeks. The theraphosids encountered during this study often built their retreats on the upper banks of creeks, hence they may come in contact with suitable substrate only short

distances from their burrows. One spider in this study (#6) had its retreat under a large stone near the bottom of a dry creek, surrounded by a substrate theoretically allowing for digging up prey. Australia's large sandy areas, and also more humid habitats like the wet tropics, may also allow for digging up prey in this manner.

Whether theraphosids can differentiate between vibratory signals generated by surface or subsurface prey at various depths, has not been tested. As I have not found any studies comparing the vibratory signals generated by surface and subsurface prey animals it is also unknown what cues might enable them to do so.

I formulated the following question to explore if theraphosids can detect the depth of sub-surface vibratory stimulus and vary their predatory responses accordingly:

Can the spider use its legs to create a 3D image of the position of the vibration source relative to the spider.

- H_0: The spiders cannot get a 3D image of the position of the vibration source.
- H_1: The spider can get a 3D image of the position of the vibration source.

Prediction: prey burrowing too deep in the substrate for easy capture will be ignored.

8.2 Results:

Eight spiders were tested. Three of these spiders completely ignored the turning propellers, at any depth. These spiders were excluded from the results.

From all the remaining 5 spiders, the propellers triggered clear orientation responses, the spiders performed a "step by step" orientation and placed themselves with the front legs held together right above the turning propeller, in a "prepared to dig" position.

There was no digging or attack responses to the propellers at 3 cm and 5 cm depth.

All spiders first dug down to, and then attacked, the propeller at 1 cm depth.

Three spiders attacked the surface propeller directly, while two of them did not attack the propeller until it had "pushed away" all the surrounding sand, and was turning in the air. Then they attacked the foam at the point where the shaft was rotating.

These results are shown graphically in figure 8.1:

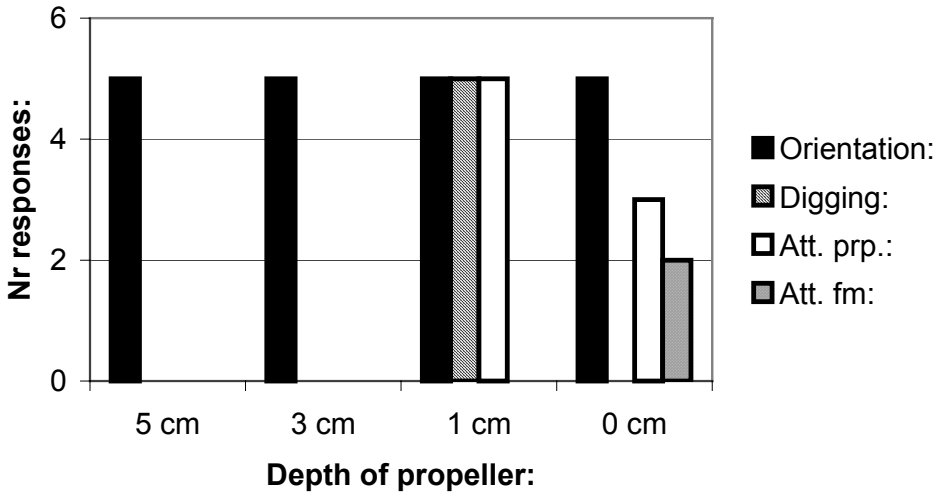


Figure 8.1: Results, predatory responses of (n = 5) spiders to arrhythmically turning propellers at various depths in substrate. Att.prp. = attack propeller, att. fm = attack foam.

8.3 Discussion:

8.3.1. General discussion:

Initially I was concerned that the spiders would not respond naturally to the vibratory signals from the propellers. Three of the spiders did completely ignore the propellers, but I feel that excluding them from the results can be defended, since I was testing how the spiders would vary their response to the various stimuli and not if they would respond to this exact stimulus. All the remaining 5 spiders performed very clear orientation responses to all propellers, and the responses were remarkably similar.

The two deepest propellers (3 and 5 cm) were all clearly detected, but although the spiders homed in on the propellers, and all of them positioned themselves directly above the propeller in a "prepared to dig" position, none of them did so. Digging down 3 -5 cm in this type of substrate is a difficult process, since the edges of the hole would continually cave in. Since all spiders were clearly interested in the "prey", but chose not to try and dig it out, it seems safe to assume that they somehow detected that it was too deep for easy capture.

The spiders appeared to detect that the propeller at 1 cm depth was close to the surface, since all spiders attacked the propeller by digging very rapidly and then seizing the propeller in their fangs. Prior to digging, the spiders responded with similar orientation responses, as to the other sub-surface propellers.

Since all spiders readily dug down and attacked the propeller at 1 cm, it seems likely that the spiders could detect that the propeller was not as deep as the other two sub-surface propellers (which only triggered orientation responses) and would be within reach of a quick attack.

Although the propeller at the surface initiated orientation responses from all spiders, the spiders appeared "suspicious" of the propeller, and were somewhat reluctant to strike, compared with a more "strike first - ask questions later"-like attitude towards live prey animals as stimulus (Chapter 7). It is possible that the vibratory signal from the propeller at surface level has a detectably different "signature" to that of e.g. walking crickets, and that this causes the spiders to bide their time. I have observed similar "suspiciousness" in many other captive and wild theraphosids while trying to tease them

out of their burrows with a straw. Responses vary from lightning fast attacks, to spiders retreating; some spiders also ignoring the straw.

However, after several minutes, three of the spiders attacked the surface propeller with the same speed and force, as observed when capturing live prey (Chapter 7). The remaining two spiders did nothing until the propeller had pushed away all the surrounding sand, and was rotating in free air. Much to my surprise, they then attacked the foam where it was traversed by the propeller shaft, instead of striking at the propeller. The turning propeller would generate low frequency air vibrations but these were ignored or not detected at all, while even the tiny vibrations made by a wire rotating inside a body of foam, was sufficient to initiate an attack. This illustrates that substrate-related vibratory cues are the primary means of detecting prey.

I would, however, expect higher frequency air vibrations, like that from a buzzing fly, to initiate predatory attacks.

All spiders seemed aware that the signal from this propeller was coming from surface level, since none of them showed any sign of digging or even preparing to do so.

How the spiders manage, at least roughly, to detect the depth in the substrate of the stimulus is not known. One can easily imagine several mechanisms, some of which I mentioned in Chapter 2. Undoubtedly there are other, possibly more correct, theories. A carefully planned experiment needs to first explore what kinds of vibratory signals are generated by sub-surface disturbances, and then to explore what cues the theraphosid spiders, and possibly many other ground-dwelling predatory arachnids, use to estimate stimulus depth. Similar capabilities may be found among some insects, e.g. parasitic wasps, that are able to locate hosts burrowing within fruit or logs (Hanks et al 2001).

It should be noted that none of the spiders spent any time turning in circles above the propeller as if searching for surface prey, like Brownell (1984) reported for some desert scorpions. My impression is that the theraphosids from an early stage detected that the "prey" was below ground.

Australian theraphosids, like many captive overseas species, readily dig to capture subsurface prey. This makes me expect that the "digging response" is a very ancient behavioural characteristic, probably present in many primitive arachnid species.

It could be interesting to try similar experiments with different types of substrates, e.g. moist dirt, and with other spider species. As in the previous chapter, it appears that theraphosid responses to vibratory signals are complex, and present a field well worthy of further research.

8.3.2. Conclusion:

Australian theraphosids respond to both subsurface and surface vibrations.

When presented with vibrational sources at various depths in a “river sand” substrate the spiders showed orientation responses to vibration sources from surface level down to as deep as 5 cm below the surface.

Prey capture responses (digging down and biting the vibration source) did not occur if the source was deeper than 1 cm below surface level. This may indicate that depth of burrowing prey can be detected.

The spiders do not evidently respond to low frequency air vibrations.

Chapter 9: Other observations

In this section I describe some behavioural observations that are not directly connected to my experiments, but may still be of some interest.

9.1. Use of silk:

Theraphosids have never been observed to use silken snares to capture prey, by spinning silken structures where prey animals become entangled, stuck in sticky silken threads, or otherwise have their movements hampered. However, they still use silk in many aspects of their daily life.

9.1.1. Silken curtains:

Similar to Minch's (1978) observations on *Aphonopelma chalcodes*, and mentioned briefly by Kotzman (1990) on *Selenocosmia stirlingi*, my observations of Australian theraphosids (both captive and in the field) and on other captive overseas species, indicate that theraphosids, as a rule, cover the entrance to their retreat with a curtain of silk when they have finished their active period, and return to their retreat during the day. The curtain may deter small animals like ants, but since it is relatively fragile, it is questionable if it serves any function in physically deterring large predators like e.g. centipedes or scorpions. Another option is that it helps maintain a higher humidity level within the retreat by reducing air circulation during the day, but this awaits further studies.

9.1.2. "Urticating moulting cradle"

It is well known that captive theraphosids often construct a thick "bed" of silk, upon which they lie when they moult (personal observation, Bruins 1999 and Schultz & Schultz, 1998). It appears that at least one species has taken this behaviour a step further. A captive *Theraphosa leblondi* was observed while constructing its moulting cradle. Several times during the construction phase, it was seen using its 4^{th} leg to carefully brush off a good dosage of urticating hairs onto the silken sheet. Movements were similar to those used when brushing off hairs towards an attacker, but were much calmer and more careful,. As a result the hairs did not travel far before settling onto the sheet. The spider would brush off some hairs, spin some more silk, brush off some more

hairs, until it was finished with its "cradle". It then immediately rolled over onto its back for moulting. The purpose of this behaviour is unknown, but it seems likely that the hairs somehow gives the spider some additional protection during the very vulnerable period of moulting.

9.1.3. "Washing the floor":

Silk may also be used to remove debris from the burrow floor, although I have only one clear observation of this. A captive *Grammostola spatulata* was seen covering the entire floor of her retreat with a layer of sticky silk before she immediately gathered up the silk and all loose particles with it. The silk was formed into a ball, picked up in the chelicera and carried out of the burrow to the far end of the terrarium, leaving the burrow completely void of prey remnants. The spider performed this behaviour several times a year (pers. obs.).

9.2. "Plugging" the retreat entrance:

Although unlike many trap-door spiders, theraphosids do not construct elaborate doors to their retreat, it appears that they can deliberately clog-up the entrance to the retreat with soil and debris mixed with silk, during special vulnerable periods. In the laboratory and earlier among my pet spiders, this was often observed prior to moulting. In the field, one spider (*Selenocosmia stirlingi*) had closed up its retreat in a similar fashion. The plug was not perfect, and in between sand, dirt and silk, I could see several tiny spiderlings moving around. This behaviour has also been reported by Kotzman (1990).

9.3. Drinking rainwater:

One night during my field observations of a large *Selenotypus plumipes* (10 Nov. 2001) there was a 20 minute period of light rain followed by a 25 minute shower of heavy rain. Temperature at surface level dropped from 27.5 ˚C before the rain, to 22 ˚C towards the end of the heavy rainfall. The spider maintained its position at the burrow entrance during the light rain. When the heavy shower started the spider first retreated, but soon reappeared and was seen separating its chelicerae and pressing its prosoma towards the bottom part of the tunnel (that opened up at a slight angle to the substrate). It could be that the spider was supporting the tunnel entrance, preventing it from collapsing, but I find it more likely that it was in fact drinking the rainwater. However, it held this position only for a couple of minutes, before it began remodelling its tunnel entrance, utilizing the temporary availability of soft soil.

9.4. Threats to theraphosids:

Finally, I wish to address the idea that Australian theraphosids, already coping with survival in a harsh habitat, may find their numbers threatened by several factors.

During my field observations cane toads (*Bufo marinus*), an animal introduced to Australia in 1935, were by far the most commonly seen animals, appearing in such large numbers that it seems likely that they are greatly reducing prey availability, especially during the dry season.

Theraphosids are also becoming increasingly popular as “pets”, which has led to large numbers of spiders being caught in the wild for overseas and domestic markets.

Sadly, most people wanting a theraphosid want a “big nasty animal” to show off. This means that adult females and males are removed from their natural habitats in large numbers. It is estimated that a total of as many as 10,000 spiders may be taken every year (Raven, 2002), and it is feared that we may, a few years down the track, see a rapid decline in some populations. If this trade is to continue captive breeding programmes will be needed to avoid damaging wild populations. Problems with transfer of animals to areas outside their natural range will also need to be addressed.

Chapter 10: Discussion and conclusion.

10.1. General discussion:

10.1.1. Introduction:

Early in the project I learned that there was only limited scientific knowledge on most aspects of theraphosid behaviour. I tried to plan my research in a manner so as to clarify many aspects of their predatory behaviour and form a general body of knowledge. I hoped to raise interesting ideas and to identify areas suitable for further studies. While this allowed me to study a wider range of questions, time limits prevented me from exploring each topic in greater detail.

10.1.2. Practical aspects and problems.

In behavioural laboratory experiments, it is (of course) of vital importance that the experimental animals behave "naturally". It became apparent that I had underestimated the need for a "field-like" retreat, in order to ensure normal behaviour by captive spiders. Compared to the spiders I studied in the field, the captive spiders spent a lot of time walking around exploring their terrarium. Initially I thought they were exploring their surroundings in search of prey, but their behaviour was in sharp contrast with field observations. When towards the end of my project, I provided a "field-like" artificial burrow, the spiders promptly stopped exploring their surroundings, and like the spiders in the field spent their active time close to the retreat entrance.

It seems clear that in order to expect natural behaviour by captive specimens, it is absolutely necessary to provide suitable "field-like" conditions. In the case of burrowing theraphosids this would include either a deep artificial tunnel, or a suitable substrate so that the spider can construct its own retreat.

It proved very difficult to predict how long it would take to complete the various experiments. This was due to variable activity levels among captive spiders. Theraphosids are long-lived animals, capable of surviving long periods without eating. This may be reflected in their behaviour. Surprisingly often, compared to spiders in the field, spiders held in the laboratory would not appear outside their retreat at all for

several nights in a row. Since all my experiments were based on voluntary spider activity, this often led to serious delays. This is most notable in the "hole in the ground set-up" where I had to end the experiment due to time constraints, even though I was still not satisfied with the amount of data collected. Likewise, this "spider inactivity problem" is the reason why most of my experiments are limited to only five replicates.

10.1.3. Locomotory behaviour.

This was perhaps the most disappointing of my results, since I hoped to find wild spiders wandering in search for prey, to study search patterns, efficiency and navigation. Early laboratory experiments seemed very promising, with spiders being surprisingly active and walking considerable distances every night. However, these findings were in strong contrast to my field observations, where spiders seemed very reluctant to venture far from their burrow.

As mentioned in section 10.1.2, the moment the captive spiders were given a more natural retreat they stopped wandering around in their terrarium, and began to hunt from the retreat entrance in a manner similar to spiders observed in the field.

A natural explanation to this is that the spiders in the laboratory were not wandering in search of prey, but were actually looking for a more satisfactory retreat.

The specially made cardboard retreat (See section 3.1.2.1.) was not accepted as a satisfactory dwelling, even though it was both dark and of the right size. However, it was different from natural burrows in two important aspects. Firstly its opening opened horizontally onto, instead of vertically up from, the substrate, and secondly, and probably more importantly, it provided very little protection against dehydration. The last point is strengthened by the fact that I had to provide drinking water in order to prevent spiders dying from dehydration.

Although my studies failed to confirm that theraphosids wander in search of prey, it should be noted that my results show that these large spiders do have the capacity to wander long distances, several nights in a row, without stopping for more than brief periods.

Field observations were conducted mainly in harsh conditions in the dry season, and it is possible that the spiders may be more active in the wet season when conditions are more favourable.

10.1.4. Senses and prey detection:

Both discovering and explaining various predatory behaviours, requires background knowledge of what senses the spider uses to detect prey, and what information is available to the animal through these senses to influence their behavioural response.

Generally speaking, vision, chemical cues, and vibrations (including sound) are the most widely used cues by which predators detect their prey (additional cues include e.g. detecting the body heat from endothermic animals)(Schmidt-Nielsen 1997). I decided to explore, in turn, the importance of these three most common types of stimulus in prey detection by theraphosids. I also considered exploring the possibility of theraphosids detecting body heat from e.g. nearby mice, but this was abandoned due to time limitations.

I had not anticipated theraphosids to have acute vision, and to use visual cues in a manner similar to jumping spiders (Salticidae) and wolf spiders (Lycosidae). But considering the absolute size of their eyes, and their placement that indicates a wide field of view, it was still slightly surprising to find that not even relatively large and active animals like a mouse, appeared to be detected at all. However, theraphosid vision does appear to serve some function in determining ambient light levels, thereby influencing circadian rhythms.

Having ruled out vision as means of detecting prey, I went on to explore the importance of chemical stimuli, as this is a well-developed sense in many arthropods. Although not considered important for most spiders, it was nevertheless a theory that had not been tested on theraphosids. Considering that theraphosids often prey on “smelly” animals like mice and other small mammals, I thought it possible that they had developed senses that would enable them to detect e.g. small mammals. Although spiders did not respond to the mouse, I found that they would detect and readily eat pieces of raw meat, which tells us not only that they can detect food items via tacto-chemical cues, but also that vibrational cues are not essential in order to recognize food.

In retrospect, it seems clear that it would have been better to have spent more time studying prey handling and responses to various vibratory stimulus, than searching for evidence of vision and chemical senses. However, I still think my reasoning for performing the experiments were correct, and it must be stressed that knowing something after it has been tested is not the same as knowing it was true all along. Although negative these results are still useful. For example, the spiders' ability to detect that prey is subsurface, might have been explained as due to vision, if this hadn't already been excluded, thereby forcing us to look for other explanations. However, concerning the visual experiment I should probably have tested the spiders with a mouse first, and then aborted the experiment upon finding no response. This would have freed more time for other studies.

Having ruled out vision and chemical senses as being important in detection of live prey, it seemed clear that theraphosids, like most other spiders, used prey-generated vibrations as their primary means of detecting prey. I went on to explore this in more detail, which led to perhaps my most interesting findings. Sadly, for some of the experiments, I was not able to collect a satisfactory amount of data. This forced me to be somewhat careful so as to not overestimate the reliability of my findings. However, some of the trends seemed quite clear.

Responses to vibrational stimuli were found to be complex. Perhaps the most interesting of my findings, was that theraphosids appear to detect differences in vibrational "signature" from various stimuli, and vary their predatory response accordingly. This included not only a capacity for detecting differences between vibrational signals from prey animals and abiotic stimuli like falling sticks, but also showed that the spiders could differentiate between vibratory signals originating at the surface and at various depths in the substrate.

Trying to determine how accurately the spiders could detect the position of surface prey proved somewhat more difficult. Not only did I have only a limited number of responses to study, but it was also difficult to extract reliable data from the recordings.

Since an attack response (prey-captures and prey-capture-responses) was found to be dynamic instead of a simple "strike", it was difficult to determine when a response to a given position of the prey started and ended. In addition it was unavoidable to use some

degree of subjective judgement when measuring angles and distances. Finally, my calculations were based on the assumption that the spider aimed to hit the prey directly with its fangs. If, in fact, the spiders aimed to strike the prey with their front legs, my measurements would be more unreliable. However, great care was taken to minimise these problems when analysing data, so I expect the results to be fairly representative, although some spiders will probably respond to prey at longer detection distances.

Although my findings should be considered a strong trend and not established facts, there was a notable similarity between my findings on theraphosids and studies made on scorpions. This could indicate that these two "primitive arachnids" may have a rather similar system for detecting and interpreting vibratory signals.

The various aspects of prey handling was another area where I feel I have only just "scratched" the subject and I suspect that theraphosids may show variations in how they manipulate and kill various types of prey. This might be especially interesting with regards to vertebrate prey, as numerous reported observations indicate snakes and mice to always be bitten in the neck and to die very quickly.

10.1.5 Fieldwork:

"Real time" observations of theraphosids in the field proved to be a very time consuming process. It requires a lot of patience and concentration from the observer, since one has to stay constantly alert for hours on end, simply because predatory responses happen quickly and may be over in a couple of seconds. Although my fieldwork gave me only limited behavioural observations of predatory responses, it allowed me to draw important conclusions by comparing behaviours of wild and captive spiders.

10.1.6. Recommendations for further research.

Considering the results from my project and the general theoretical background, it is clear that several areas are in need of further studies. I expect it will prove particularly interesting to explore how theraphosid predatory responses are influenced by various vibratory stimuli. Both the sensory capabilities and behavioural responses have yet to be explored in detail. Similarly, the physical characteristics of vibratory stimuli, and how theraphosids use these characteristics to extract information, need to be explored in

order to explain e.g. how these spiders seemingly are able to detect the depth of burrowing prey, or can differentiate between a falling leaf and a falling stick.

Several other aspects of predatory behaviour remain unknown, e.g. methods of handling various prey, detection and capture of flying prey, and the importance of "taste" to determine palatability of food items.

10.2. Overall conclusion:

I feel my study has succeeded in forming a general body of knowledge, identifying interesting aspects of theraphosid behaviour, that may function as a foundation for future more specialised projects.

- Australian theraphosids predominantly hunt by ambushing prey near their refuge.
- Vision and chemical senses appear not important for detecting live prey.
- Prey is detected by air- and substrate-borne, prey-generated, vibrations.
- Depth of burrowing prey appears to be detected.
- There is a strong indication that theraphosid spiders can vary their response, according to various "signatures" of abiotic and biotic vibratory stimulus.
- Prey capture appears to be dynamic, including re-orientations towards fleeing prey and manipulation of prey by legs and pedipalps before fang insertion.

Prey handling and responses to various vibratory stimuli appear complex and are recommended for future research projects.

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Appendix 1: Locomotory behaviour

Table 1.1: Results from observations in individual holding terraria.
S = spider number, Loc. = Locomotory, Stat. = Stationary

S	Date:	Distance: (m)	Time usage: (h:mm) Loc. act.:	Stat. act.:	Inside retreat:	Spinning act.:	Comments:	Emerged first at:
10	15.des.00	0,05	00:00	00:00	09:55	00:05		20:01
10	18.des.00	3,59	00:35	09:25	00:00	00:00		Pre 20:00
10	16.jan.01	13,8	01:26	00:15	08:18	00:01		Pre 20:00
10	17.jan.01	0	00:00	00:00	10:00	00:00	Not seen	
4	20.des.00	7,55	01:07	07:52	00:37	00:24		20:35
4	21.des.00	4,74	01:03	04:38	04:14	00:05		Pre 20:00
4	22.des.00	3,84	00:33	04:40	04:46	00:01		Pre 20:00
4	23.des.00	5,26	00:51	07:28	01:12	00:29		Pre 20:00
7	24.des.00	47	03:07	00:05	06:48	00:00		20:01
7	25.des.00	113	05:31	00:06	04:12	00:11		Pre 20:00
7	26.des.00	79	04:07	02:24	03:12	00:17		Pre 20:00
7	27.des.00	75	04:07	00:34	05:16	00:03		20:11
2	02.jan.01	4,65	00:32	05:39	02:57	00:52		21:02
2	03.jan.01	2,68	00:12	01:50	07:48	00:10		21:34
2	04.jan.01	4,63	00:23	06:47	02:38	00:12		20:21
2	05.jan.01	2,98	00:09	03:51	05:25	00:35		Pre 20:00
3	06.jan.01	0	00:00	00:00	10:00	00:00	Not seen	
3	07.jan.01	6,35	00:42	00:00	09:18	00:00		Pre 20:00
3	08.jan.01	2,38	00:24	00:00	09:36	00:00		23:30
3	10.jan.01	4,13	00:40	06:31	02:49	00:00		22:50
5	12.jan.01	11,74	00:57	00:15	08:48	00:00		Pre 20:00
5	13.jan.01	0	00:00	00:00	10:00	00:00	Not seen	
5	14.jan.01	0	00:00	00:00	10:00	00:00	Not seen	
5	15.jan.01	0	00:00	00:00	10:00	00:00	Not seen	

Locomotory activity:

Defined as all periods where the spiders was mainly moving around, and although they frequently made small pauses, none of theese exeeded 10 min.

Stationary activity:

Defined as all periods where the spiders did not move across the substrate, they could be sitting completely still, or preform stationary activities like washing.

Table 1.2: Results from observations in large terrarium.
S = spider number, Loc. = Locomotory, Stat. = Stationary

S	Date:	Distance: (m)	Time usage: (h:mm) Loc. act.:	Stat. act.:	Inside retreat:	Spinning act.:	Comm-ents:	Emerged first at:
19	26.feb.01	0	00:00	00:00	10:00	00:00	Not seen	
19	27.feb.01	0	00:00	00:00	10:00	00:00	Not seen	
19	28.feb.01	84,3	03:24	02:26	04:09	00:01		20:32
19	01.mar.01	0	00:00	00:00	10:00	00:00	Not seen	
19	02.mar.01	86,6	02:43	00:10	07:04	00:03		22:40
7	12.mar.01	0,5	00:06	09:54	00:00	00:00	Ex. Intr.	Pre 20:00
7	13.mar.01	0,1	00:00	09:14	00:45	00:01	Ex. Intr.	Pre 20:00
7	14.mar.01	0,2	00:00	09:55	00:01	00:04		Pre 20:00
7	15.mar.01	0,1	00:00	10:00	00:00	00:00		Pre 20:00
7	16.mar.01	0,1	00:00	10:00	00:00	00:00		Pre 20:00
21	19.mar.01	38,4	02:40	00:00	07:17	00:03		22:55
21	20.mar.01	41,7	01:49	00:00	08:11	00:00		21:36
21	21.mar.01	95,1	02:54	00:00	07:06	00:00		23:35
21	22.mar.01	120,7	04:57	00:01	04:59	00:03		20:48
21	23.mar.01	23	01:54	00:11	07:54	00:01		20:58
2	26.mar.01	0,3	00:00	08:12	01:36	00:12		21:22
2	27.mar.01	40	02:04	05:34	02:15	00:07		Pre 20:00
2	28.mar.01	0	00:00	09:03	00:54	00:03		Pre 20:00
2	29.mar.01	26,3	02:10	00:19	07:27	00:04		Pre 20:00
2	30.mar.01	34,4	02:35	00:04	07:17	00:04		Pre 20:00
4	02.apr.01	53,4	02:41	02:25	04:53	00:01		Pre 20:00
4	03.apr.01	27,4	01:54	00:05	07:57	00:04		00:11
4	04.apr.01	57	04:14	00:10	05:34	00:02		20:52
4	05.apr.01	30	01:39	06:19	02:02	00:00		21:46
4	06.apr.01	10,1	00:40	05:28	03:52	00:00		23:52

Locomotory activity:

Defined as all periods where the spiders was mainly moving around, and although they frequently made small pauses, none of theese exeeded 10 min.

Stationary activity:

Defined as all periods where the spiders did not move across the substrate, they could be sitting completely still, or preform stationary activities like washing.

Appendix 2: Visual experiment

Table 2.1: Results from visual experiment, p 1/2.

S = spider number, St.entr = sitting in retreat entrance, In retr. = in retreat.

	S	#1 Visit:	1st visits:		Tot. visits:				
			Stim:	Ctrl:	Stim:	Ctrl:	Middle:	St. entr:	In retr:
Fan:									
Right side:	19	control	1	1	2	3	6	2	3
	7	stimulus	3	0	4	3	0	4	4
	20	control	0	1	0	2	2	1	2
	2	control	0	1	0	1	3	3	3
	21	control	2	5	27	25	26	8	9
Left Side:	19	stimulus	1	0	2	1	5	2	2
	7	control	1	2	5	5	1	4	4
	20	stimulus	1	0	1	1	2	1	2
	2	control	2	1	74	73	9	4	4
	21	stimulus	10	0	28	24	24	11	12
10xMb:									
Right side:	19	control	1	5	10	13	21	6	6
	7	stimulus	2	2	23	21	9	5	5
	20	stimulus	1	0	6	3	7	2	2
	2	stimulus	4	1	5	5	7	5	5
	21	control	12	3	32	24	28	15	16
LeftSide:	19	stimulus	5	2	10	9	20	8	8
	7	stimulus	3	1	25	25	5	3	4
	20	control	0	1	0	1	2	1	2
	2	control	2	3	63	65	8	4	5
	21	stimulus	9	2	65	61	27	9	12
2xCr:									
Right side:	19	control	2	2	21	20	13	4	5
	7	stimulus	2	3	9	8	1	5	6
	20	control	0	3	4	6	11	3	4
	2	na	0	0	0	0	0	2	2
	21	control	1	4	19	21	23	5	6
Left side:	19	stimulus	3	0	5	2	6	3	3
	7	control	2	3	6	9	2	5	5
	20	stimulus	1	0	1	1	2	1	2
	2	stimulus	3	2	95	92	17	5	5
	21	stimulus	4	1	42	39	11	5	6
Mouse:									
Right side:	19	control	1	6	8	10	16	8	8
	7	stimulus	3	2	8	8	4	5	5
	20	stimulus	1	1	1	1	3	1	2
	2	na	0	0	0	0	1	2	3
	21	stimulus	4	3	22	20	20	5	8
Left side:	19	stimulus	2	2	7	5	11	5	5
	7	control	3	3	14	16	3	7	8
	20	control	0	1	1	1	1	0	2
	2	stimulus	3	0	4	0	4	4	4
	21	stimulus	6	1	24	21	12	7	8

Table 2.1: Results from visual experiment, p 2/2.

S = spider number, St.entr = sitting in retreat entrance, In retr. = in retreat.

	S	Tot. time:					Date:
		Stim:	Ctrl:	Middle:	St. entr:	In retr:	
Fan:							
Right side:	19	0:03:41	0:12:15	0:52:10	1:24:06	5:27:48	24.jan.02
	7	0:21:30	0:36:32	0:00:00	5:28:49	1:33:09	09.jan.02
	20	0:00:00	0:05:55	0:01:16	0:01:06	7:51:43	12.feb.02
	2	0:00:00	0:01:34	4:40:23	1:54:54	1:23:09	02.feb.02
	21	1:13:25	1:18:21	1:03:00	0:56:10	3:29:04	07.feb.02
Left Side:	19	0:03:04	0:02:56	0:09:42	4:35:28	3:08:50	26.jan.02
	7	0:29:19	0:24:09	0:13:35	5:21:23	1:31:34	08.jan.02
	20	0:03:20	0:03:59	0:02:22	0:00:40	7:49:39	08.okt.01
	2	1:43:33	3:07:32	0:11:13	0:54:22	2:02:20	22.aug.01
	21	0:55:00	1:34:02	0:09:16	0:38:37	4:43:05	16.aug.01
10xMb:							
Right side:	19	0:43:18	0:38:56	4:00:38	1:02:56	1:34:12	15.jan.02
	7	1:39:07	1:21:24	0:21:38	3:23:06	1:14:45	13.jan.02
	20	0:19:47	0:18:15	0:06:12	4:47:55	2:27:51	10.feb.02
	2	0:13:26	0:09:49	0:11:52	5:49:45	1:35:08	31.jan.02
	21	1:51:51	1:08:54	0:22:32	1:13:52	3:22:51	05.feb.02
LeftSide:	19	0:57:41	0:21:07	0:22:19	4:21:47	1:57:06	16.jan.02
	7	4:34:32	1:51:52	0:03:34	0:11:58	1:18:04	12.jan.02
	20	0:00:00	0:47:57	0:04:36	0:01:14	7:06:13	10.okt.01
	2	1:55:34	3:03:40	0:04:59	0:08:21	2:47:26	20.aug.01
	21	2:34:18	4:05:31	0:18:26	0:08:32	0:53:13	14.aug.01
2xCr:							
Right side:	19	1:30:06	1:17:13	0:49:23	1:25:34	2:57:44	17.jan.02
	7	0:36:37	0:30:23	0:02:56	5:07:25	1:42:39	07.jan.02
	20	0:09:17	0:28:41	0:13:27	0:01:55	7:06:40	11.feb.02
	2	0:00:00	0:00:00	0:00:00	06:22:03	01:37:15	01.feb.02
	21	1:04:57	1:15:50	1:36:02	0:05:43	3:57:28	06.feb.02
Left side:	19	1:35:50	0:10:25	2:09:28	2:34:44	1:29:33	18.jan.02
	7	0:33:05	4:57:55	0:07:24	1:08:33	1:13:03	06.jan.02
	20	0:18:59	0:53:40	0:03:19	0:01:08	6:42:54	12.okt.01
	2	2:15:49	3:09:11	0:15:14	0:39:47	1:39:59	21.aug.01
	21	2:06:35	2:21:58	0:10:23	0:09:04	3:12:00	15.aug.01
Mouse:							
Right side:	19	0:19:23	0:28:11	0:29:37	5:13:13	1:29:36	19.jan.02
	7	0:54:55	4:48:04	0:11:26	0:44:29	1:21:06	11.jan.02
	20	0:05:06	0:04:49	0:03:37	0:00:43	7:45:45	16.feb.02
	2	0:00:00	0:00:00	3:39:12	1:36:56	2:43:52	03.feb.02
	21	1:16:11	0:50:17	1:08:40	0:03:56	4:40:56	08.feb.02
Left side:	19	1:25:56	0:13:29	0:48:50	3:43:35	1:48:10	20.jan.02
	7	0:51:44	0:56:40	0:03:02	4:30:44	1:37:50	10.jan.02
	20	0:29:11	0:03:41	0:00:27	na	7:26:41	07.okt.01
	2	1:49:38	0:00:00	1:12:23	2:58:40	1:59:19	23.aug.02
	21	1:44:58	1:30:20	0:05:00	0:10:16	4:28:53	17.aug.01

Appendix 3: Olfactometer experiment

Table 3.1: Results from olfactometer experiment, p 1/2 S = spider number.
KeepCo = keeping container, In retr = in retreat.

	S	#1 Visit:	1st visits:		Tot. visits:				
			Stim:	Ctrl:	Stim:	Ctrl:	Tunnel:	KeepCo:	In retr:
Control:			Right	Left	Right	Left			
	6	left	6	7	13	12	28	14	0
	24	right	8	1	11	6	18	14	6
	2	right	5	1	9	7	13	7	1
	21	right	4	2	8	7	14	8	1
	19	right	16	4	26	19	42	28	8
Meat:									
Right side:	6	stimulus	5	11	14	15	36	18	0
	24	stimulus	8	4	14	9	27	13	0
	2	control	7	1	8	5	17	25	10
	21	stimulus	6	5	8	12	24	13	1
	19	stimulus	16	0	18	8	35	18	1
LeftSide:	6	stimulus	9	4	11	7	28	15	0
	24	control	5	19	22	27	53	25	0
	2	stimulus	2	3	8	9	14	7	2
	21	stimulus	15	3	21	12	37	19	1
	19	control	7	9	17	18	36	17	1
Cr:									
Right side:	6	stimulus	9	15	18	25	53	28	0
	24	stimulus	10	4	17	13	30	15	0
	2	stimulus	5	4	13	14	21	11	2
	21	control	6	3	10	10	19	10	1
	19	stimulus	8	4	15	10	27	14	1
Left side:	6	control	17	12	32	29	65	34	0
	24	control	1	15	11	21	36	17	1
	2	control	4	4	10	10	18	9	1
	21	stimulus	4	5	8	9	18	12	2
	19	stimulus	3	2	5	5	11	6	1
Mouse:									
Right side:	6	stimulus	7	3	16	15	27	17	3
	24	stimulus	18	7	45	31	57	42	12
	2	control	5	2	14	12	17	9	2
	21	stimulus	8	1	15	10	20	12	2
	19	stimulus	5	0	6	4	11	8	2
Left side:	6	stimulus	7	10	24	22	37	28	6
	24	control	4	15	25	26	48	21	1
	2	stimulus	1	4	8	9	12	13	5
	21	stimulus	6	0	20	15	16	7	1
	19	control	10	12	22	21	49	23	1
Spider:									
Right side:	6	stimulus	4	1	7	5	13	6	0
	24	stimulus	19	1	22	15	45	21	1
	2	stimulus	7	1	11	7	20	13	4
	21	stimulus	13	4	19	13	38	18	1
	19	stimulus	13	6	19	17	38	22	2
Left side:	6	control	1	1	2	1	4	3	0
	24	stimulus	10	18	30	34	68	29	0
	2	stimulus	1	0	2	1	2	3	2
	21	stimulus	4	6	16	18	20	11	2
	19	control	8	12	17	22	43	22	1

Table 3.1: Results from olfactometer experiment, p 2/2 S = spider number. KeepCo = keeping container, In retr = in retreat.

	S	Tot. time:					Date:
		Stim:	Ctrl:	Tunnel:	KeepCo:	In retr:	
Control:		Right	Left				
	6	0:37:08	0:40:20	0:04:33	6:37:59	0:00:00	25.okt.01
	24	0:15:22	0:10:38	0:01:12	1:51:36	5:41:12	07.des.01
	2	0:21:38	0:18:31	0:28:10	5:00:49	1:50:52	17.des.01
	21	0:10:53	0:08:36	0:02:00	2:13:50	5:24:41	28.jan.02
	19	0:22:42	0:19:05	0:08:26	3:16:51	3:52:56	05.feb.02
Meat:							
Right side:	6	0:54:01	0:56:50	0:11:42	5:57:27	0:00:00	05.nov.01
	24	0:16:40	0:12:38	0:02:59	7:27:43	0:00:00	11.des.01
	2	0:18:33	0:14:19	0:02:31	1:27:30	5:57:07	20.des.01
	21	0:16:18	0:18:25	0:04:26	4:21:31	2:59:20	25.jan.02
	19	0:31:11	0:10:11	0:08:53	2:34:35	4:35:10	15.feb.01
LeftSide:	6	0:34:09	0:13:50	0:05:09	7:06:52	0:00:00	06.nov.01
	24	0:33:46	0:55:04	0:07:07	6:24:03	0:00:00	10.des.01
	2	0:11:10	0:14:32	0:02:44	4:37:37	2:53:57	21.des.01
	21	0:38:43	0:27:23	0:06:11	3:25:26	3:22:17	24.jan.02
	19	0:22:06	0:33:53	0:15:15	2:29:36	4:19:10	13.feb.02
Cr:							
Right side:	6	0:30:21	0:47:59	0:07:08	6:34:32	0:00:00	23.okt.01
	24	0:29:07	0:18:52	0:03:39	7:08:22	0:00:00	06.des.01
	2	0:10:17	0:12:41	0:04:08	6:30:40	1:02:14	15.des.01
	21	0:16:31	0:16:14	0:03:35	4:35:32	2:48:08	19.jan.02
	19	0:21:12	0:14:49	0:08:45	2:32:05	4:43:09	02.feb.02
Left side:	6	1:11:50	0:48:04	0:08:07	5:51:59	0:00:00	24.okt.01
	24	0:17:44	0:40:39	0:07:30	6:49:32	0:04:35	05.des.01
	2	0:11:21	0:09:32	0:03:37	4:56:00	2:39:30	16.des.01
	21	0:07:38	0:14:56	0:03:22	4:09:12	3:24:52	17.jan.02
	19	0:04:56	0:07:15	0:05:54	1:14:37	6:27:18	03.feb.02
Mouse:							
Right side:	6	1:03:46	1:40:01	0:04:15	3:11:35	2:00:23	22.okt.01
	24	1:09:22	1:00:10	0:08:56	4:55:40	0:45:52	03.des.01
	2	0:23:41	0:22:03	0:03:37	3:47:26	3:23:13	14.des.01
	21	0:24:30	0:14:59	0:03:31	3:36:05	3:40:55	15.jan.02
	19	0:09:36	0:06:19	0:04:38	1:11:31	6:27:56	31.jan.02
Left side:	6	1:26:30	2:08:20	0:06:56	2:29:20	1:48:54	21.okt.01
	24	0:28:00	0:43:53	0:08:57	6:26:53	0:12:17	04.des.01
	2	0:21:27	0:20:57	0:01:46	4:07:03	3:08:47	13.des.01
	21	0:50:55	0:27:19	0:02:45	4:22:58	2:16:03	16.jan.02
	19	0:38:20	0:39:48	0:42:13	3:33:17	2:26:22	29.jan.02
Spider:							
Right side:	6	0:13:48	0:24:27	0:02:43	7:19:02	0:00:00	07.nov.01
	24	0:29:19	0:22:39	0:05:34	6:57:12	0:05:16	08.des.01
	2	0:31:00	0:11:39	0:23:48	3:21:22	3:32:11	18.des.01
	21	0:29:59	0:15:03	0:05:05	4:16:36	2:53:17	21.jan.02
	19	0:24:38	0:21:17	0:11:30	3:46:13	3:16:22	12.feb.02
Left side:	6	0:03:35	0:01:15	0:00:39	7:54:31	0:00:00	26.okt.01
	24	0:47:16	0:54:08	0:10:44	6:07:52	0:00:00	09.des.01
	2	0:04:16	0:00:41	0:00:16	2:29:16	5:25:31	19.des.01
	21	0:32:42	0:38:55	0:03:02	5:57:11	0:48:10	20.jan.02
	19	0:25:18	0:34:43	0:10:17	2:30:47	4:18:55	06.feb.02

Appendix 4: Prey capture experiment

Table 4.1: Results for prey capture precission experiments in the "hole in the ground" set-up, p 1/4.
S = Spider nr. ss = stick small Ls = leaf small crS = cockroach small
c = cricket sl = stick large LL = leaf large crL = cockroach large
cr = cockroach WC = web cut rl = "rattling" leaf BB = big beetle
pc = prey capture pcm = prey capture movement
pcr = prey capture response intrr = interrupded movement

Det.dst. = Detection distance (cm).
Chel.dst. = Cheliceral distance (cm).
Rst.dst. = Rest distance (cm), set to "u" if <=2cm.
Det.ang. = Detection angle (degrees).
Rst.ang. =Rest angle (degrees), set to "na" if stimulus position was innside spider legs.
(Terms are further explained in section 7.7.2.)

S	Type:	Det.dst.:	Chel.dst.:	Rst.dst.:	Det.ang.:	Rst.ang.:	Comment:
19	BBpc	1,9	8,7	u	18,3	na	dragged beetle into hole
	c1pc	8,8	15,2	intrr	149,2	intrr	prey jumped into spider
	c1pcr1	0,9	4,4	u	31,8	na	s strikes to left side, misses
	c1pcr2a	1,3	6,4	intrr	140,7	intrr	pcm towards mov. prey at rear/right
	c1pcr2b	9,1	13,5	5,3	89,1	48,1	pcr after fleeing prey
	c1pcr3	3,8	9,6	u	62,7	na	pcr front/left, misses
	c1pcr4	4,2	8,5	5,4	76,5	131,2	pcr front/right, misses
	c2pc	2,4	5,8	u	72	na	pc left side
	c2pcm1	1,4	6,4	5,6	11	13,3	short forward movent after prey
	c3pc-pcm1	4,9	8,2	4,62	46,4	33,7	slowly to front left
	c3pc	1,2	6	u	10,7	na	short strike after prev. c3pc-pcm1
	c3pcm1a	17,8	22,4	16,4	110	49,3	1st of two orientations
	c3pcm1b	11,1	15,9	11,8	49,3	0,6	2nd of two orientations
	c3pcm2	9	13,5	11	9,3	8,9	short forward movement
	c3pcm3	20,3	25,1	18,6	46	10,1	cricket fell from roof, far front right
	c3pcm4	11,6	17,5	9,5	87,6	11,4	landing cricket far front left
	c3pcr1	5,1	9,9	u	4	na	foreward pcr
	c3pcr2	7,9	13,1	5,3	178	11,8	over hole
	c3pcr3	15,8	22	7,9	16,3	23,3	forward run
	c3pcr4-pcm1	8,9	13,3	8,5	113,3	58,7	slow right turn
	c3pcr4	3	7,6	u	58,7	na	short strike right
	c3pcr5-pcm1	5,3	7	4,6	179,7	91,5	over hole
	c3pcr5	0,9	5,5	u	91,5	na	strike left
	crLpcr1	1,7	4,6	u	20,6	na	strike foreward
	crSpc	6,1	11,3	3,4	77,8	na	cr fell from roof
	crSpcm1	5,8	9,5	4,2	124,7	53,2	delayed response
	crSpcm2	6,4	10	5,8	76,8	28,4	slightly delayed response
	crSpcm3	5,8	11,1	9,3	3,7	25,31	slow response
	crSpcm4	8,5	12	7	37	4	via and measured on leaf
	crSpcr1	1,1	6	1,7	22,4	na	short strike
	crSpcr1.pcm1	19,5	23,9	21,3	22,6	32,2	slow re orientation
	crSpcr2	2,4	5,5	u	70,2	na	slow, lousy pcr
	crSpcr3	1,9	5,3	2,7	84,7	na	short half harted movement
	crSpcr4	11,3	17	unavail	46,7	unavail	landing c, 2nd pic wrong pic…
	crSpcr6	4,1	8,5	u	5	na	via and measured on leaf

Table 4.1: Results for prey capture precission experiments in the "hole in the ground" set-up, p2/4.

S	Type:	Det.dst.:	Chel.dst.:	Rst.dst.:	Det.ang.:	Rst.ang.:	Comment:
19	LL1	4,5					pcr
	LL2	12,2					pcr
	LL3	7,1					pcr
	LL4	5,8					pcr
	Ls1	4,9					pcr
	Ls2	13,5					pcr
	Ls3	23,6					no response
	Ls4	0					pcr
	sl1	22,96					no response
	sl2	24,16					no response
	sl3	20,5					no response
	sl4	20,9					no response
	ss1	6,8					pcr
	ss2	17,4					no response
	ss3 1st impct	21,85					no response
	ss3 2nd impac	4,9					pcr, ss landed on sL
	ss4	23,9					no response
	rl1	15,78					no response
	rl2	17,6					no response
	rl3a	17,21					fast pcm
	rl3b	11,1					fast pcm then retreated slowly
	rl4	5,7					no response
	rl5	6,3					no response
	rl6	5					no response
30	c1pc	2	4,8 u		91,4 na		pc left
	c2pc	2,7	5,08 u		92,7 na		tracks rng pr without stp to re orintat
	c2pcm1	11,8	15,2	13,4	69,9	75,4	slow movement up from hole
	c2pcr1	2,3	5,5	3	39,9 na		halfharted pcr
	LL1	2,2					pcr
	LL2	15,8					unprecise pcm/pcr
	LL3	7,6					pcr
	LL4	17,2					no response
	Ls1	17,1					pcr
	Ls2	na					no response, bur resp to wall (me?)
	Ls3	14,6					no response
	Ls4	22,6					no response
	sL1	16					no response
	sL2	26					no response
	ss1	25,9					no response
	ss2	25,8					no response
31	c1pc	1,7	2,5 u		4 na		close to hole
	c1pcr1	1	2,5 u		94,7 na		pcr right
33	c1pc	0,6	36 u		59,9 na		pc left
	c1pcm1	4,1	5,4	5	84,6	64,8	short pcm
	c1pcm2	3	5,6	2,9	79,5 na		pcm left
	c2pc	2,9	6,3 u		68,8 na		short chase
	c2pcr1	2,5	5,2	2,5	136 na		near 180 turn
	c3pc	3,1	6,7 u		93 na		precise pc
	c3pcr1	6	8,2	6,7	54,9	95,2	from inside hole
	crSpcr1	4,51	7,91	1,6	34 na		via leaf

Table 4.1: Results for prey capture precission experiments in the "hole in the ground" set-up, p 3/4.

S	Type:	Det.dst.:	Chel.dst.:	Rst.dst.:	Det.ang.:	Rst.ang.:	Comment:
33	crLpcr1	8,62	11,6	1,5	75,6	na	via leaf
	crLpcm1	14,3	16,7	15,2	108,7	51,2	via leaf
	LL1	15,6					no response
	LL2	6,5					pcr
	LL3	16,7					no response
	LL4	1					pcr
	Ls1	6,8					pcr
	Ls2	6,9					pcr
	Ls3	14,4					no response
	Ls4	5					pcr
	sL1	27,7					no response
	sL2	24,4					no response
	sL3	28,7					no response
	sL4	25,8					no response
	ss1	25,9					no response
	ss2	20					no response
	ss3	25,8					no response
	ss4	25,9					no response
42	c1pc	3,3	6,4	3,6	42,3	27,9	front left
	c1pcr1	2,2	4,4 u		108,5	na	left
	c2pc	3,7	7,3 u		117,3	na	short left
	c2pcm1a	12,2	13,8	13,1	79,1	34,3	from hole
	c2pcm1b	14,2	17,33	15,7	56	44,5	front right
	c2pcm2	**26,2**	30,2	24,8	50,2	27,9	turned 78,1
	c3pcr1a	4,4	6	4,6	76,2	48,5	short slow
	c3pcr1b	1,9	4,8 u		49	na	unprecise
	crlpcm1	8,1	10,3	7,6	16,7	4,4	from hole
	crlpcr1	4,7	6,4 u		22,1		
	crlpcr2	2,6	7,1	3,8	55,2	na	front right
	crlpcr3	2,6	5,4 u		14,7	na	cr on tape
	crlpcrLeafrel	8,7	12,7	3,5	62	na	via leaf
	WCcpcr1	3,2	6 u		2	na	strait
	WCcpcr2	2	5,6	2,2	116	na	right rear
	WCcpcr3	25,61	31,4	22,3	8,4	2,9	far front
	WCcpcr4	2,5	4,2 u		14,7	na	from hole
	WCcpcr5a	1,8	5,6 u		141,8	na	right rear
	WCcpcr5b	3,5	7	1,6	98,9	na	halfharted
	WCcpcr6	2	6,7 u		138,5	na	rear left
	LL1	2,7					pcr
	LL2	16,7					no response
	LL3	11,7					retreat
	LL4	1,9					pcr
	Ls1	23,8					delayed pcm
	Ls2	7,9					pcr
	Ls3	27					delayed pcm
	Ls4	9,1					delayed pcm
	sL1	24,3					no response
	sL2	23,5					delayed pcm
	sL3a	16,9					no response
	sL3b	1,5					pcr on scnd imp
	sL4	24,15					no response

Table 4.1: Results for prey capture precission experiments in the "hole in the ground" set-up, p 4/4.

S	Type:	Det.dst.:	Chel.dst.:	Rst.dst.:	Det.ang.:	Rst.ang.:	Comment:
42	ss1	21,9					no response
	ss2	23,4					no response
	ss3	20,7					no response
	ss4	19,9					no response
	rl1	20					no response
	rl2	19,6					no response
	rl3	19,9					no response
	rl4	13,3					retreat
	rl5	4,4					retreat
	rl6	5,3					no response

Appendix 5: Behavioural categories

Listing of various behavioural charactheristics, based on personal observations of captive and wild spiders. Used in order to take quick notes during video analysis and field observations:

- **Sitting, (st):** - body is resting on the substrate.
- **Standing, (sta):** - body is held clear of the substrate.
- **Sitting inside retreat entrance, (stiRe):** - sitting motionless just inside the retreat entrance, with no legs protruding past the tunnel opening.
- **Sitting in retreat entrance, (stRe):** - sitting motionless with its 1^{st} 2^{nd} and 3d pairs of legs spread out on the substrate. The 4^{th} pairs of legs are still inside the burrow opening.
- **Sitting at retreat, (staR):** - sitting motionless just outside the retreat entrance, with all legs clear of the tunnel opening.
- **Exploring, (ex):** -walking around, but making frequent short pauses where the spider "freezes". None of these pauses exceeds 10 min.
- **Drinking, (dr):** – lowers the front end of its prosoma into the water, moves chelicera apart and sits motionless. Small rhythmic movements can bee seen on the palps and to a lesser extent the legs.
- **Washing, (wa):** -stands still, preforming a "dance like" cleaning ritual in which one leg at a time is carefully cleaned with saliva, using the chelicera and fangs. Legs are also wetted with saliva, and then used to clean other legs or the abdomen. Legs are brushed against each other in a manner that will remove any particles.
- **Spinning, (sp):** - producing silk while normally moving the abdomen from side to side. Often walks forward at the same time.
- **Spinning in circles, (spc):** -moves around its own axis, while spinning. Normally used to wrap silk around large prey items, or to construct an egg sac.
- **Spinning at retreat, (spaR):** -spinning a sheet-web on the ground near the retreat entrance, and \ or constructing a nice funnel like webbing around the entrance.
- **Spinning at retreat entrance, (spRe):** -seals up the entrance with a fine curtain of silk, either in one ore several layers. Normally done when the spider has finished its active period.

- **Feeling behaviour, (fb):** -stands with body held high on the second third and fourth pair of legs. First pair of legs are lifted as high as possible, and then slowly lowered in a forward arch, while the spider leans forward on its legs. The spider then moves one step forward or sideways, and the behaviour is repeated.
- **Tapping:** First pair of legs is forcefully slammed down on the substrate, both legs hitting the ground at the same time.
- **Prey capture movement, (pcm):** -moves slowly to orient itself with front end towards a potential prey item.
- **Prey capture response, (pcr):** -lunges forward at high speed, trying to capture prey.
- **Prey capture, (pc):** -successful prey capture.
- **In retreat, (iR):** - is inside its retreat, not visible.
- **Threat display:** - stands on third and fourth pair of legs, raises the 1st and sometimes the 2nd pair high in the air. Body is held at 45 to 90 degrees to the substrate and the fangs are displayed, with more aggressive species having drops of venom at their tips